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Editor **M. R. D. Seaward.** MSc, PhD, DSc, FLS. The University, Bradford BD7 1DP

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Subscriptions should be sent to:

Mr Richard Comley, 1 Highfield Rise, Stannington, Sheffield S6 6BS

All other YNU matters should be addressed to:

Mr John A. Newbould, Tapton House 30 Moorlands, Wickersley
Rotherham S66 0AT

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FROM CONEY TO RABBIT: THE STORY OF A MANAGED COLONISER

A. HENDERSON

Presidential address presented to the Yorkshire Naturalists' Union at Beverley, 7 December, 1996

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"Thys hand kan ferette in konnyngherys"
John Lydgate
The Pilgrimage of Man (1426)

Introduction

To find a rabbit native to the part of the world we nowadays call the British Isles, we would need Dr Who's Tardis to carry us over 10,000 years back before the close of the Pleistocene Age when, the fossil record shows, the rabbit became extinct here and throughout most of Europe, surviving the Ice Ages only in the milder region of the Iberian peninsula. This was the part of their known world, their mappamundi, that the ancient Greeks and Romans regarded as its home: in the words of Catullus, in the last century BC, '*Celtiberia cuniculosa*', the rabbit-teeming Spanish peninsula.

From the Mediterranean to Britain

The animal's nuisance value was already recognised. Catullus' contemporary, the Greek historian Strabo, describes how the colonists of the Balearic Isles petitioned the Emperor Augustus to rid them of this pest or find themselves other territory. Later, in the 1st century AD, Pliny the Elder recounts how the walls of Tarragon succumbed to undermining from rabbit-burrowing: a reverse story to that of the geese which saved Rome. However, the quality of the animal's meat and fur were reckoned to be redeeming features. Catullus, admittedly in fiercely satiric mood, describes the debauchee, Thallus, as '*mollior cuniculi capillo*', softer than the rabbit's fur. The Roman epicure chef, Apicius, includes rissoles of rabbit (prized less than those of peacock or pheasant, but above those of chicken or tender sucking-pig) amongst his recipes. Awareness of these favourable characteristics and of the animal's sporting potential led the Romans to place the rabbit alongside the hares which, as Varro describes, they were already keeping in leporaria or hare-warrens. Eventually, when more exotic animals were added to their populations, some of these warrens became, in effect, vivaria or virtually game-reserves: perhaps we should really think of them as prototypes of Whipsnade with the rabbit and hare in lieu of wallabies. Although Roman law stipulated that game was *res nullius* (finders and catchers keepers), the existence of such private leporaria shows that this was not entirely without qualification. From the Mediterranean and southern France rabbit-warrens spread steadily through much of western Europe, reaching Germany (*e.g.*, the island warren at Schwerin-See in 1407) (Zeuner, 1963) and Hungary (Margaret Island in Budapest, originally called Rabbits' Island) (Bökönyi, 1974). At some time in the 11th or 12th century the Normans introduced the animal into Britain, and by the mid-13th century there were rabbit-warrens as far north as Crail and Cramond in Scotland (Gilbert, 1979) and as far west as Ballysax and Rosslare in Ireland (Hayes, 1965) (Fig. 1).

Early iconography

Data on the rabbit's early days in Britain are scattered, often brief mentions in the diverse historical record. Perhaps some of the most delightfully informative notions we can arrive at come from its entry into ecclesiastic and other iconography. It is surely serendipitous that this talk is being given in St Mary's parish hall, Beverley, St Mary's being the home of

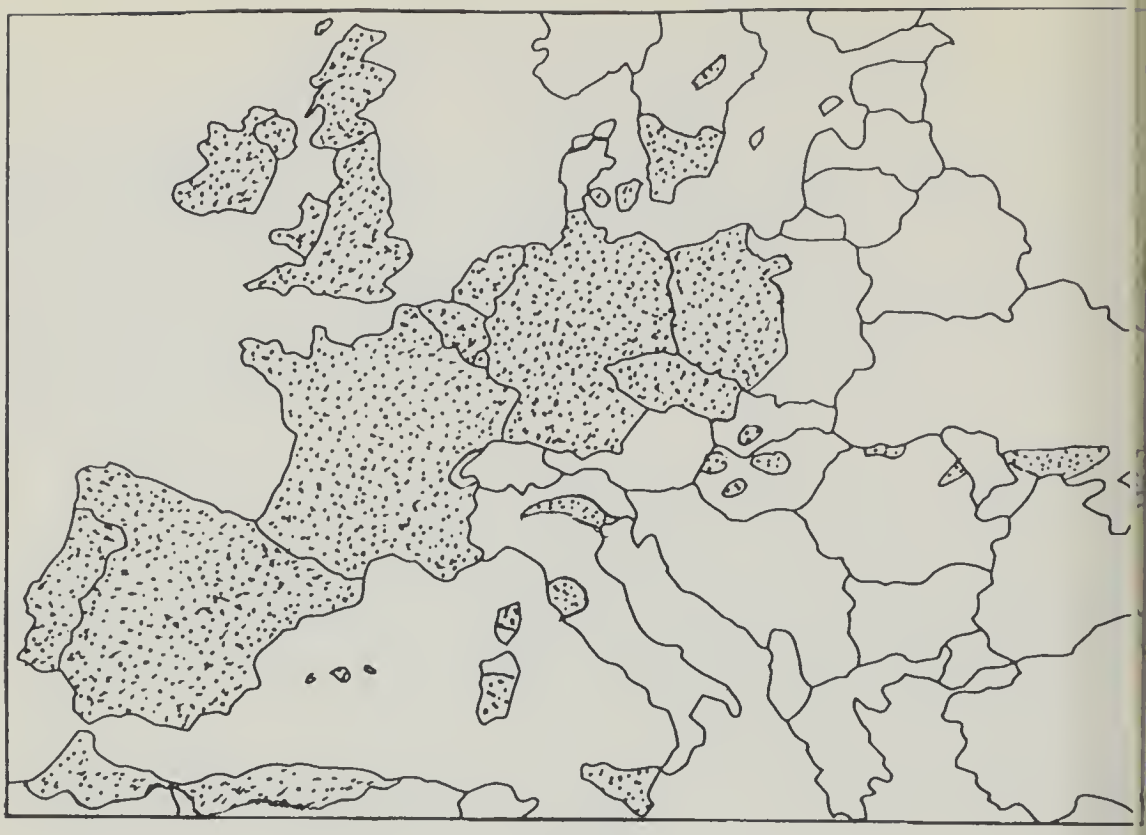

FIGURE 1
Distribution of the rabbit in Europe and North Africa.
From Biadi, F. (1993) *Le lapin de garenne*. Office National de la Chasse.

one of the county's most well-known figures of a rabbit (Fig. 2), sculptured about 1325, but probably better known now than then, as it is rumoured to be the source of inspiration for Tenniel's White Rabbit in Carroll's Alice story, a distinction well-deserved by this proud specimen of *Oryctolagus cuniculus*, the tunnel digging hare, as his Greek and Latin roots define him. On late medieval tiles of the 13th century or just after (Williams, 1985), unearthed during the restoration of Bangor cathedral in the 1890s, he is seen emerging from his burrow in repeat pattern. At Kilpeck church, Hereford, one of seventy 12th century carvings on the corbel table (Fig. 3) is possibly the earliest sculptural likeness of a rabbit in Britain, certainly one of the most engaging and Disneyesque. Particularly informative, however, is one of the hagiographic illustrations (Fig. 4) to Lydgate's life of the holy English king, St Edmund, which shows his miraculous recapitation. When the king was attacked and overpowered, his head was severed from his body, and this narrative scene pictures both a guardian wolf presenting the lost head to a team of ministering monks, and the moment of reattachment. The incident is reputed to have occurred in 835 AD, but the 15th century miniaturist has pleasingly and anachronistically set the event in a 15th century coneygarth or rabbit-warren, giving us one of the best intimations we have of such early managed warrens. Other pictures of the time show woven wattle fencing, brushwood or other thick hedging bounding enclosures where conies thrive. In Queen Mary's Psalter (Warner, 1912) women are represented catching conies with ferrets and nets, and engaging in what one can only call a coney-bashing exercise! Even amongst ground game conies were usually accounted of low status by mediaeval nobility and gentry, and it may be that machoism as well as male chauvinism considered it woman's work to catch conies for the table, etc., in the nearby coneygarth.

FIGURE 2
The Pilgrim Rabbit, St Mary's Church, Beverley: carved *c.* 1325, and reputed to be the inspiration for Lewis Carroll's White Rabbit. Photo: Chris Hairsine.

FIGURE 3
Rabbit and dog sculpture from the corbel table of Kilpeck church.
From: *The Sculptures of Kilpeck*; © Reg Boulton. 1987.

FIGURE 4
The recapitation of St Edmund. A 15th century miniature, illustrating Lydgate's *Life of St Edmund*. By permission of the British Library: Harley MS 2278 f 67v.

Etymology

In Middle English the rabbit was known as 'coney' or 'cunning', derived from the Old French nouns 'connil' and 'connin'. A rabbit-warren or earth was, therefore, a 'cunning-erthe', leading to the later commonly occurring form, 'coneygarth'. This and the Latin 'coniger' (= 'coneygarth') lead to such common corruptions as 'conigree', 'coninger', 'cunnery', etc. At first, the term 'rabette' referred only to the young rabbit, 'coney' referring to the adult animal. Eventually the terms 'coney' and 'rabbit' became interchangeable, until today, of course, 'rabbit' is our usual name for the animal at all ages.

Indication of warren sites

Cartographic names can be effective indicators of the sometime presence of a coneygarth or rabbit-warren. Generally, such names as 'coneygarth', 'conigree', etc., 'warren', 'warren house, farm or hill', etc., are signs of one-time managed rabbit activity, although such *double entendres* as 'coney', very occasionally deriving from the Teutonic root 'koenig' (= 'king'), and 'warren' after the Earls Warenne and their kin, are grounds for caution. Such indicators can then be checked in likely documentary sources, such as Charters, Patent Rolls, Inquisitions post Mortem, tithe and enclosure maps with the accompanying awards, estate maps, terriers, manor extents, leases, etc. References may also be found in local and personal records, diaries, notebooks and correspondence, game registers, kitchen

accounts, etc. The reliability of initial cartographic indications is evidenced by the frequency with which further documentary or field searches yield supporting proof of the existence of a managed warren in a given area at a given time. Such sites are, indeed, commoner than might at first be supposed. That part of Yorkshire lying west of York has already yielded evidence of 130 such one-time warren sites. Equally important methods of detection and exploration are provided by fieldwork and the consultation of aerial photographs. These can reveal the presence in a landscape of some of the warren features and artefacts now to be described.

Warren structures and artefacts

The situation of warrens and the structures and artefacts within them, large and small, are governed by topographic, geo-edaphic, economic and practical agricultural dictates, which has led to considerable individualisation in their establishment and realisation. The large county of Yorkshire is fortunate in having representatives of a wide range of warren forms and artefacts.

Boundaries

Hurrell (1979) has drawn attention to the earliest known record of rabbits in Britain, in 1135 AD on Drake's Island in Plymouth Sound, when ownership of the island was transferred to Plympton Priory *'cum cuniculi'* [sic] (= with the rabbits). Several of our earliest warrens were on islands, where an open or largely unenclosed warren was provided with natural boundaries against rabbit escape and predator intrusion. Thus, the Countess of Arundell's 'conny warrin' on the south-western point of Hayling Island (East, 1891) required the erection of only a short length of artificial boundary (a mere seventh of the total perimeter). The earliest record of a mainland warren cited by Hurrell is a deed of transfer for a Dartmoor warren, in the area of the later Trowlesworthy Warren, vaguely dated as 'drawn up' sometime between 1135 and 1272'. There are certainly other records within this interim (for instance, a royal order of 1240 (*Cal. Cl. Rolls, Henry III 1237-1242*) to allow W. de Ferrariis to take 20 live rabbits from the Wirral; another order of the same date for 100 rabbits to be taken by Hugo le Franceys from Dorking and Reigate; and orders of 1235 for 10 live rabbits and of 1242 for 30 or 40 rabbits from the cunnery in the park at Guildford). Domesday Book does not mention any rabbit-warren, but interestingly lists one hare-warren at Gelston, Lincolnshire, a precursor of numerous later hare-warrens, such as one on the Isle of Purbeck during the reign of King John, when Purbeck was a forest with a ranger and two warreners preventing poaching of 'coneys, hares, foxes and pheasants' (Hyland, 1978), one at Hampton Court in the 16th century and several in post-mediaeval Wiltshire.

Like insular warrens those on the mainland coast made use of the sealine as a natural boundary. Such warrens, however, often entailed considerable boundary construction, utilising whatever materials were at hand locally. Warrens in general were mainly situated on marginal economy land of low fertility. (Hence, later, the development of the vast commercial warren complexes that occupied thousands of acres on Dartmoor, in the East Anglian Breckland, on the East Riding Wolds and the North Riding Tabular Hills, where they reached from Hutton-le-hole to Hackness (Harris & Spratt, 1991). They were frequently on rougher upland sites or, if lowland, on sandy, gravelly or heathland areas. Earthen or sod embankments were constructed to serve as convenient and necessary boundaries in many such cases, topped by growing gorse or thorn below a cap of turf (Figs. 5 & 6). Crackles (1993) has pointed to the importance of gorse as winter fodder for managed rabbits, and notes the use of gorse faggots as bearding on the top of warren sod walls, overhanging the inner face to prevent rabbit escape. In regions like Yorkshire and Dartmoor, where stone was available, stone walls or revetted embankments were employed as well. Like earthen embankments they might also be used to construct smaller internal breeding and feeding enclosures within the larger warren territory, such as the four newtakes known as the Four Aces, still in good preservation and visible over long distance at Headland Warren, Dartmoor.

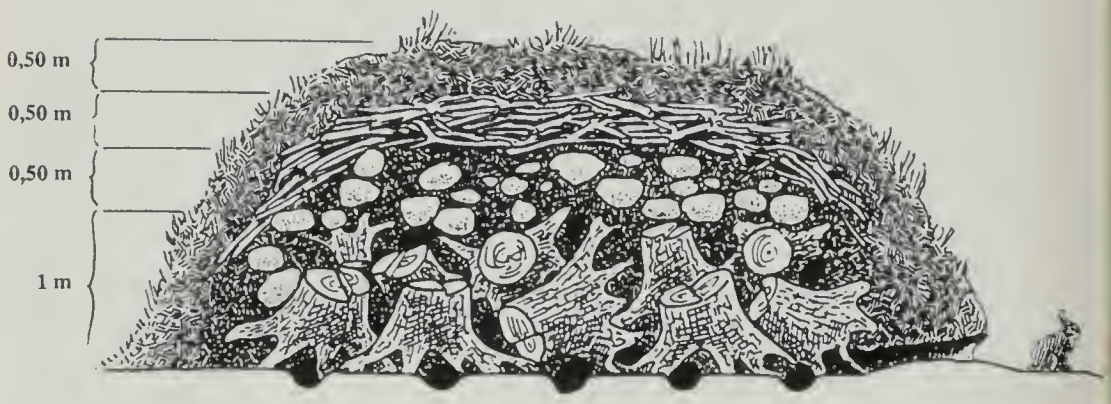

FIGURE 5
Peripheral warren wall, constructed of tree-stumps, stones, twigs and cloth, covered with light non-clayey earth, and roofed with stout branches and a variety of plants.
Biadi, F. (1993) *Le lapin de garenne*. Office National de la Chasse.

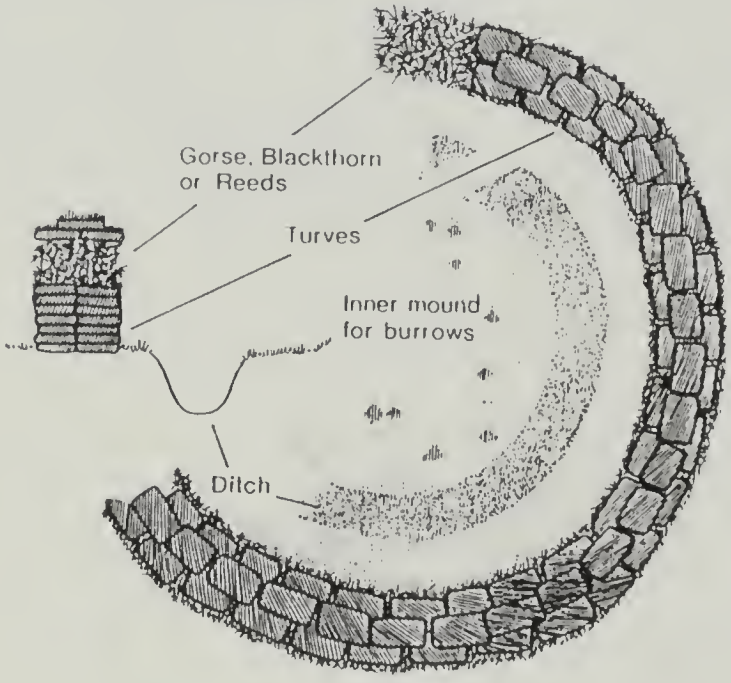

FIGURE 6
Reconstructed warren, Knettishall Heath.
By permission of Suffolk County Council, Graphics Section (G. Wade, artist).

Lodges and other warren houses

The most upstanding feature of the warren landscape was the lodge or warren house. Since the demise of warrens, such lodges as remain often stand in a landscape that has progressed one way or another to woodland, and they have lost some of the stark dominance that led Shakespeare to describe Claudio as 'melancholy as a lodge in a warren'. Forest lodges, such as the Royal Hunting Lodges of King John and Queen Elizabeth were primarily

directed towards the pursuit of higher game and enjoyment of the chase. Queen Elizabeth's Lodge, indeed, is reputed to have had an open-sided first storey for viewing the full panoply of the passing hunt in comfort. The role of belvedere or gazebo was doubtless one played at times by many lodges, but usually, like the warren house proper, their major role was a custodial one, providing a working base for the warrener and his assistants, and for storage, gutting, packing, etc.

Thetford Warren Lodge, on brown calcareous Breckland sands, is still, despite being gutted by fire early this century, a bleak and sombre edifice, a former centre of defensive activity in a fortified warren liable to threat by armed poachers, its stout walls in the local flint. The most distinctive lodge of all architecturally is the Rushton Triangular Lodge in Northamptonshire (Fig. 7), a laudable curiosity (English Heritage, 1997), built between 1593 and 1597 by Sir Thomas Tresham in celebration and honour of the Holy Trinity, with three walls on a triangular plan, each 33 feet long and with three windows with three gables to each, three-storied and with a three-sided chimney on top. Clearly, a building of profound devotional intent in its design; but one which the Rushton accounts refer to as the Warreyner's Lodge (Finch, 1956). Manuscripts in the Public Record Office show that the warren was 300 acres and that there was also a neighbouring connegerie at nearby Pipewell. Ferrets were kept for bolting the rabbits, and boxes of rabbits and skins were despatched three times weekly to London, amounting to a lucrative business in contracts with poulterers there. The official in charge of such a warren would enjoy real status, unlike those employed merely for the ruder tasks of warrening. In Yorkshire, Norton Tower (Fig. 8) on a high

FIGURE 7
Rushton Triangular Lodge (The Warreyner's Lodge).
© English Heritage.

escarpment edge south of Rylestone, the Rylestone of Wordsworth's White Doe, is now but a ruin of its former self. It stands on old warren land with a commanding outlook over the surrounding terrain. Moorhouse (1991) has identified the site as a late mediaeval rabbit-warren and hunting enclosure, probably owing its origin to a dispute over hunting rights between the Norton family of Rylestone and the Cliffords of Skipton who held much land to the east.

In other warrening areas, of course, much less grandiose buildings can be found. One example is Ewden Cote on the Broomhead Hall estate in the Ewden valley, north-west of Sheffield. This building was used as a gutting house. Upper and lower chambers to the south have well-flued fireplaces for drying out hanging skins, and the building doubled as an effective shelter for shooting parties in inclement weather, as well as providing simple living quarters for a working warrener and family or his assistants. It has a covered loading bay for storage and despatch by cart of rabbits and skins.

Pillow mounds

Among the best known features of old coneygarths are pillow mounds; low mounds, usually rectangular in plan and surrounded by a ditch where earth has been thrown onto the mound, and fashioned to encourage rabbit habitation, the main aim of creating such mounds being the localisation of rabbit activity with obvious advantages for a busy warrener. Some pillow mounds consist entirely of soft or gravelly earth; others include varying amounts of stone as a constituent, larger flatstones sometimes being used to cap man-made burrows to prompt further spontaneous burrowing by the rabbits. Rounded and cairn-shaped mounds are also encountered. Moorhouse notes them near Norton Tower, and there is a small rounded mound, a low cone to the view, alongside some of the rectangular mounds at Flasby. At Merrivale Warren, Dartmoor, among many rectangular mounds one was observed that is horse-shoe shaped. Probably the finest array of pillow mounds in Yorkshire is to be seen on top of Douthwaite Dale, north-west of Hutton-le-hole (Fig. 9).

Recently, Williamson and Lovcday (1988) have studied a range of pillow mounds, *inter alia* in the light of possible confusion with similar Neolithic earthworks, etc. Examining pillow mounds at 190 sites, they found the commonest width (*c* 60% of samples) was between 4 m and 6 m, with a minimum width between 1 m and 2 m, and a maximum width of 16 m. Lengths varied from 8.4 m to 234 m. In comparison, pillow mounds seen in Yorkshire fit comfortably with their analysis.

FIGURE 8
Norton Tower, Rylestone. Photo: J. Taylor.

FIGURE 9
Array of pillow mounds on top of the escarpment, Douthwaite Dale, north of Hutton-le-hole.
By permission of the Royal Commission on Historic Monuments: RCHME.
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USE OF OLDER LANDSCAPE FEATURES

Older earthworks have not uncommonly been used later in the establishment of warrens. At Dolebury Warren, Somerset (Oxford, 1986) linear pillow mounds cross the ancient hillfort's interior. A shallow ditch surrounds each, and they reach a width of 10 m, and range in length from 15 m to 100 m, with a present height up to 1 m. At the Iron Age hillfort of Danebury, Hampshire, the area was, according to an account of 1678 (Cunliffe, 1983), 'anciently and till since the memory of man a warren and let to several tenants at rack rents and was entire to itself and (not a sheep common) had a lodge in it. Only since the rabbits were destroyed they have fed the sheep there, and when it was a warren the sheep many times went over it and not questioned because the warreners' rabbits trespassed as much on their sheep-down'. Here in Yorkshire, at Huddlestone Old Wood, near Micklefield, adjacent to Coney Garth Hill (shown on the 1850 O.S. map), lies a now thickly wooded, irregularly hexagonal embankment system, about 0.25 km^2 in area, with evidence of warrening use where a 0.5 km-long transverse internal embankment has been trenched out, the trench then capped over with flatstones and heaped over with earth.

One of the most intriguing of Yorkshire warren sites is at Cockmoor Dykes, north of Snainton on the Scarborough-Pickering road. These dykes (Spratt, 1989) form an eastern part of the extensive system of ancient dykes on the upland limestone areas, which delineate strip territories. Cockmoor Dykes is a most impressive array of twenty closely parallel ditches and banks on the Troutsdale escarpment. Spratt concluded that the six larger dykes formed part of the original boundary system, but the fourteen smaller dykes originated in the 18th century, a period of major warrening activity in this area. Today the dykes are riddled with very old and new burrows, and there is a rabbit tip-trap (see below) nearby.

Warrens have been established at a great variety of sites. At Pompocali, near Bardsey (Henderson, 1979) an old stone quarry on the Carlton Grits is named as Coney Garth Plantation on the map accompanying the Enclosure Award, and may be an instance where spontaneous rabbit colonisation invited the installation of a managed warren by the local landowner or tenant farmer. Earlier this century unemployed miners at Wilson Wood Colliery, near Clapham, created a rabbit-warren (Phil Hudson, *pers. comm.*) by digging out slag-heaps, inserting pipes and bringing in rabbits. The artificial tunnels can still be seen, though in some disrepair, and rabbits are still active on the site. One of the most unexpectedly located of mediaeval warrens is mentioned in an accounts list of 1453-1454 (Morton, 1954) for Peterborough monastery: '*Item quatuor cuniculi de cimeterio Sancti Johannis Baptistae*' (Item: four rabbits from St John's graveyard), indicating the existence of a warren in the church graveyard, now St John's Close.

Rabbit and vermin traps

Specially designed traps for rabbit and vermin were made in some regions. Tip-traps (known as 'types'), first introduced in the late 18th century (Fussell, 1955), have been fully described from the North Yorkshire Moors (Harris & Spratt, 1989), where the same term, 'type', is also used to designate the small stone-walled enclosures in which some pit-traps are located. Several types have been located on Bolton Abbey estate (detection of the first, according to reliable anecdotal account, involved the successful use of the divining rod!). In Strid Wood the types, sited immediately by stone boundary walls, are associated with small muce-holes or passages through the wall. Muce-holes (also known as 'smouse-', 'smoose-' or 'smoot-holes') are small, square, rectangular or round passageways through the base of a wall, allowing rabbit transit, at Strid Wood guiding the rabbit into a narrow tunnel with a trap-door which, when set, plunged the rabbit into the pit below. Such pits varied in size and construction, the smallest seen to date being at Cunnery Wood, Shibden Hall, Halifax, where the width of the circular aperture is about 0.6 m. The sides of this pit slope conically outward towards the base, as in types on the Yorkshire Moors. Types seen at Bolton Abbey have rectangular pits with perpendicularly upright sides and the pits approach 1 m in depth and width. Larger still are known, and rounded pits are not uncommon. Muce-holes unassociated with types were used to encourage rabbit movements during netting and other trapping.

Vermin traps developed specialised forms in some regions. Those on Dartmoor have been described by Haynes (1970). There, in general, vermin were led into hutch traps by a system of funnelling walls. At Headland Warren Dartmoor, traps were found without any such guiding walls, relying on chance, baiting or strategic positioning by muce-holes in enclosure walls.

Warreners, gamekeepers and poachers

Warreners, gamekeepers and the motley individuals who stole from them used similar methods to take their quarry. A notice of appointment of gamekeepers for his manor of Aldburgh from John Wentworth of Woolley, near Barnsley, summarises the methods and implements used (Lawson-Tancred, 1937). It authorises the appointee 'to take and levy for my use all such guns, bows, grayhounds, setting dogs, lurchers or other dogs to kill hares or coneys, feretts, tramelles, low bells, hayes or other nets, snares or other engines for the

taking and killing of coneys, hares, pheasants, partridges and other game as shall be used within the precincts of the said manor by any person or persons not having lands or tenements or some form of inheritance, in his own or his wife's right, or having lease or leases of 99 years or for any longer term of the clear yearly value of £150, other than the son and heir of an Esquire or other person of higher degree.'

This list of equipment is not radically different from that described in the 14th-century journal of the French nobleman, Sire de Gouberville (Delort, 1978): 'The coney hunt is engaged in by the nobility to the same degree or more than the lower estate. The nobility make use for such a chase of spaniels, likewise small greyhounds. One group of the animals is taken "in eourse" by fast hounds. The others shelter in their burrows. The hunters then put purse nets over the mouths of the burrows, except for one through which they put in a muzzled ferret or one with its teeth cut down (so that it doesn't beeome drunk with blood) or then they light a fire of sulphur, orpiment and myrrh on the inside of a cloth or parchment and they throw it into a vent-hole. The rabbits emerge *en masse* with the draught and are caught in the nets. In 1479, six people (including the king's jester) hunting for 2½ days and 3 nights were able to catch 72 rabbits, using 3 ferrets. For the poor, a different smoke mixture took the place of dogs and ferrets, *i.e.* old woollen rags, parchment with sulphur, orpiment and myrrh, powder in a pot provided with an iron pipe, branches of broom, linseed and chareoal.' Rabbits would be taken abundantly by such restrained methods and by netting, ensuring that the fur was completely undamaged.

Poaching

Already by John Lydgate's time, the 15th century, rabbit poaching was commonplace enough for him to use it in his long poem, *The Pilgrimage of Man*, as descriptive of Avarice's second hand:

> 'Thys hand, thogh men hadde sworn,
> Kan robbe and bern away the corn
> Out off bernys and garnerys;
> Thys hand kan ferette in konnyngherys
> Be nyhte tyme, whan men slepe;
> Thys hand by hoſys kan in crepe
> And bern a-way what he may fynde,
> And lyst to leue nothyng behynde.'

The history continues eonsistently as far as poaehing is concerned. When Charles Fothergill passed through North Dalton in 1805, his diary records his satisfaction at finding 'the whole eountry, tho so wild and open, entirely enclosed from Pocklington to Driffield (Fothergill, 1984). Even the rabbit warrens near Driffield, which last time I was here were filled with rabbits and heath, now exhibited fields of waving corn'. Not owing to inerease of profit by growing corn, 'but a gang of poachers, amounting to 26 in number, having for several years past committed so many and continual depredations insomueh as to eonsume two thirds of the rabbits, it was thought proper to destroy the remainder and turn the warrens into arable land, notwithstanding the ring-leaders of poaehers were taken and tried at the lent assizes when they were transported for 7 years'.

Disputes

Encouragement by landowners and warreners and a resulting backlash from neighbouring tenants and other affected locals have been a persistent feature of the rabbit's existence since it became established here in significant numbers, and the animal has been a frequent cause of social and legal disputation. For instanee, towards the elose of the 15th eentury during the reign of Henry VII, amongst several depositions laid against Sir Roger Hastings in the Pickering area (Turton, 1894), was the charge 'that he of newe hath enelosed within the fields of Thornton and Farmonby ii aeres and more of arrabill grounde and annexed it to a Cunnygerthe, to the gret hurt and distruccion of the King's tenantes and inhabitauntes of Thornton and Farmonby'.

Equally annoyed were the townspeople of Liscard, Cheshire, in 1754, when they arrived at what they termed a Rabbit Agreement against the local landowner, John Gough (Woods & Brown, 1960). 'Be it known to all men whom it may concern, they whose names are here under subscribed do covenant, agree with one another to destroy all the Rapits on the Warren or Coney Borrow on the Common. Whereas John Hough do claim a property of the Rapits in that Warren, which we hereafter mentioned do not allow the said John Hough to have . . . etc.'

Feelings could become even more heated. So, in the mid-18th century, John Minshull (17--) of Sunderlandwick posted up a notice to his neighbours (now in the East Riding Records Office) airing his grievances: This is to give Notice that upon Complaint of Damages by my Tenants and Neighbours which the Rabbits or otherwise Conies has made upon the Ground or Premisses of the aforesaid Tenants and Neighbours . . . Now I do hereby certify that I shall not pay one Farthing for the Damages . . . And for the Insult of my Tenants in Complaining to Me for Satisfaction I am fully Determin'd to take the Ground out of their Possession and let it to the best Bidder who will promise not to make any Complaint upon the like Occassion [*sic*]: And further, if any of the Tenants should take Kill or Destroy any Conie or Conies upon their Ground or Premisses either with Guns dogs Nets Snares or any other Invented Engine or Engines whatsoever shall suffer according to law as in that case. Item I do here [*sic*] there is a Grumbling and Complaining with the Neighbours around me about their Dogs being Killed such as Mr Dowbegin for the loss of Captain: Robert Tateson and Richard Gunlass for theirs: and William Chambers two Dogs . . . these two last dogs I suppose escaped only with peppered Arses . . . These complaints are insufferable and a man of any Spirit cannot help resenting such ill Treatment from Neighbours: I therefore but not in any Passion tho Just Reason from the afores^{d}: Complainants or Complainers do affirm that I shall or one by my order: Take Kill or Destroy: any kind of dog or dogs . . . that shall go ten Yards out of the Road to wag his tail or Piss upon Sunderlandwick Moor. Item alledging yet more if I cannot . . . destroy the afores^{d}: dog or dogs Neither with Guns Traps or Person, I shall for these dogs Trotting over or Pissing on my Grass Prosecute the Proprietor . . . as far as law will Admitt of --- John Minshull.

Four north-eastern English warrens

1. Holy Island

Today, rabbits are found on 700 of the world's islands (Flux, 1994) between latitudes 60°N and 55°S, over 300 of them being around the British Isles. Monks, sailors, island farmers, lighthouse keepers and others have contributed to this distribution. Monastic orders may have found the introduction particularly desirable and satisfying since the Church allowed the consumption of rabbit meat at times when only fish was permissible, since young rabbits, not long from the womb, were regarded as aquatic! (Biadi & LeGall, 1993).

The island nearest to the Yorkshire coast with an early warren is Holy Island; on the map (Fig. 10) it resembles a Liebig's condenser with the long neck generously jammed at the mouth. This long-necked peninsula, the Snook, and the northern coastal stretches to the east of it are the sandiest parts of the island, useless for most crops, but an ideal location for a rabbit-warren. The earliest warren reference traced so far for Holy Island is in 1377 (Raine, 1852) when it had a valuable rabbit-warren belonging to the see of Durham. The Bishop of Durham shortly afterwards caused tithe of the rabbits there to be paid to the Prior of Holy Island, and in 1438 Thomas Monckton was appointed Keepere of the Warren for life, receiving an annual fee, paid by the farmers of the warren, and 'a robe of the suit of our esquires', with the concomitant duty of supplying the Bishop's table with rabbits as required. In 1528 a 12-year lease of the rabbit-warren and borough of Holy Island was charged at £4 yearly the warren and £3 yearly the borough. In 1739 there was a lease to Jane Selby of Holy Island of the 'rocks, ware, kett [*sic*] or seaweed in Holy Island, the coney warren, the tithes of fish', etc., and the harbour dues, rents or customs paid over nine years, for £105 per annum. By 1759 the lease had increased to £130.

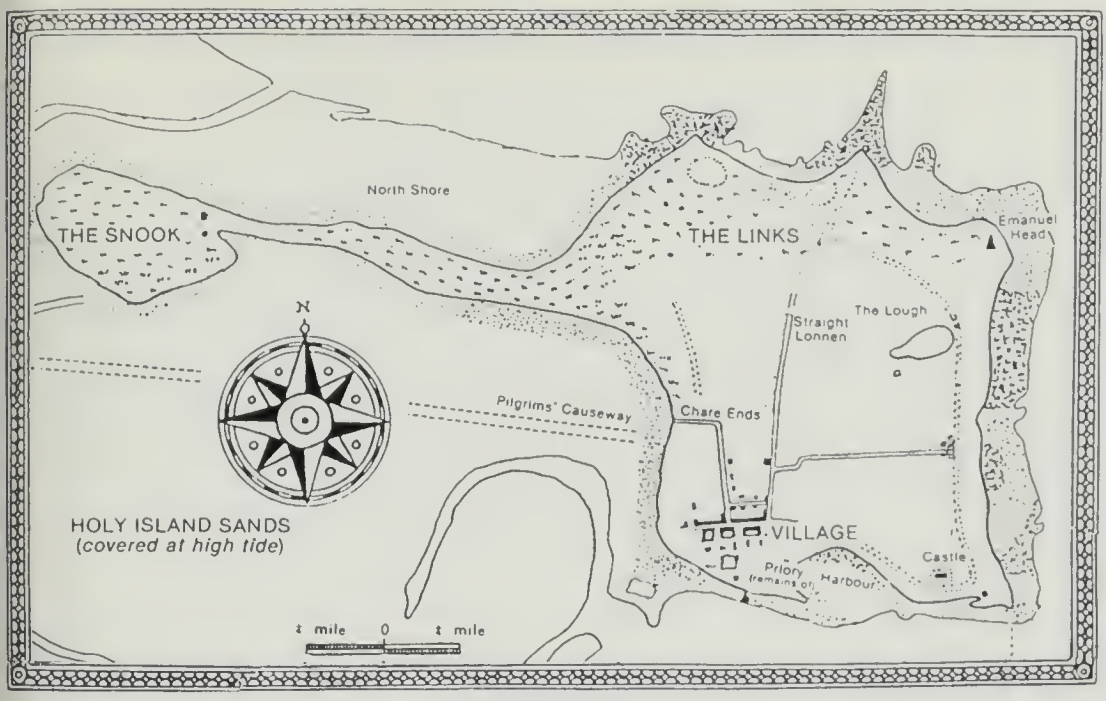

FIGURE 10
Map of Holy Island. Based on a map ©Frank Graham.

The areas of the Snook and Links were described by Winch in 1822: 'The uncultivated part of the island is sandhills or links slightly held together by the creeping roots of the sea lyme-grass, sea mat-grass, rushy wheat grass and sea carex, and is occupied as a rabbit-warren.' Another description reads: 'Without woods, moorlands or rivulets, Lindisfarne possesses a scurvy flora. Cryptogamic plants are peculiarly scarce, with the exception of the marine algae'. On the links are listed: Flat-headed sedge, Grass of Parnassus, Brookweed, Seaside Centaury, Bloody Cranesbill, Common Storksbill, Scarlet Pimpernel and Blue Fleabane, and the lone lichen listed from this part of the island, '*baeomyces alcicornis*' (= *Cladonia foliacea*).

Some ecological pros and cons of rabbit-grazing have been summed up with regard to the smaller Farne Islands to the south, where rabbits seem to have been brought in by the lighthouse-keepers as a handy food supply (Hirons, 1994). 'Rabbits can have a beneficial effect on the vegetation. They help maintain floral diversity by removing tall grasses, they produce lawn-like areas of turf. Their wastes help fertilize the soil and disused rabbit-burrows can be used by puffins for nesting. Their harmful effects are most conspicuous when numbers become high: damage to vegetation by overgrazing and trampling; the young shoots are damaged . . . By eating seedlings rabbits prevent many species becoming important components of the vegetation cover. By scraping and burrowing, the soil is exposed and desiccates'.

2. Holderness

In coastal mainland regions, too, many areas of dune, sandy links and lowland were favoured warren sites, for instance, the chains of warrens along the Lancashire coast, and along the East Anglian sandlings. Some of Yorkshire's earliest warrens were on the Holderness lowlands in the region of Spurn's predecessor, 'Alde Ravenser'. A royal mandate of 1303 (Cal. P. Rolls 1301-1307) empowers 'Richard Oysel and Ralph de Lellay to enquire touching malefactors in the King's free warren at Brustwyk, Preston, Kayngham, Little Humbre, Burton Pydese, Skipse, Esington, Skeftling, Kilnese and

Wythornese; persons who carried away hares and rabbits from the said warren'. A royal writ of 1306 to the same Richard Oysel, seneschal, states: 'The King has two coneygarths, that is the west coneygarth, and the east coneygarth in Esington and Kilnese by Alde Ravenser on Humber, with warren in the same. The King gives to the warrener keeping the great west coneygarth, 26s 8d a year, that is 6d a week, and 6s 8d yearly for his robe; and to a lad (gareioni) keeping the small eastern coneygarth, 13s a year, that is 3d a week.' Quite how much earlier rabbits were stocked in Holderness remains doubtful, but among those assisting the steward and sheriff, as early as 1150, were warreners and falconers with sport in their care. In 1214 (English, 1979) there is mention of a warrener, Augustine, and a little later of a staff including four warreners; while in the sheriff's accounts of 1261-1264 the keeper of the warren receives the same 6s 8d for his robe as mentioned above. A late 13th to early 14th valuation of Kilnsea (at £30 to £40 net) says that £2 of this was for the herbage of the warrens. Beside this herbage rent, money was reeeived from rabbit sales (292 in 1296-1297; but only 38 in 1348-1349 when manorial income was redueed by the sea encroaching). Crackles (1993) points out that it is not clear whether the warren herbage consisted of Gorse or Sea Buekthorn or both: and notes a bylaw at Keyingham in 1637 stipulating that the inhabitants should 'dike and beard their land with thornes, furres or suehlike'. The warren at Kilnsea was not closed down until the 18th eentury.

3. Woodhall Warren

Woodhall Warren, near Carperby, also variously named as Nappa Warren and Lady Hill Warren, is situated on the north bank of the Ure, just west of Aysgarth (Fig. 11). It oeeupies a glacial area containing a 38 m high drumlin, Lady Hill, near its eentre (Yorkshire Dales National Park, 1996). To the north runs the Askrigg-Carperby road. In 1251-2 (Whaley, 1890) Henry II made a grant of free warren at Woodhall (such a grant conveyed the right to hunt all small game, suehas foxes, hares, pheasants, partridges, squirrels, rabbits, etc., but is, of course, not *per se* proof of rabbit presenee in the locality at the time of the grant).

In 1890 Whaley described the warren of siver-grey rabbits then operating at Woodhall as very ancient, but a plan of 1756 whieh matehes the area of the warren, gives no indication of warrening aetivity. Jeffery's 1771 map marks the area as warren, but without any marking of boundaries. However, Alexander Fothergill in his diary writes on 21 February 1757: '. . . to Woodhall Park where Robert Dent and Robert Durham met mee to take Hutehinson House to rebuild for the warrener' (Fothergill, 1985). This is the house now known as Warren House, situated in Hutchinson Close, and it appears that warrening may have begun at Woodhall some time earlier. All the referenees traeed would fit in with Hartley and Ingilby's statement that it was probably started by Thomas Metcalf of Nappa Hall, who lived from 1687 to 1756. On Metealf's death there was considerable change on the Woodhall estate.

On 13 May 1756 Fothergill viewed the premises at Woodhall Ings to divide them between George Metealfe and Solomon Beezon. Almost twenty years later he reeords obtaining a rent of £19. 7s from John Dinsdale for the Woodhall Park (so called), noting that they want a good wall at the bottom of the Intake that they may propagate a breed of rabbits there to keep down the whins, etc. On 28 Oetober 1774, about eight months later, he reeords the same rent collected from John Dinsdale for Woodhall Warren. The 1856 O.S. map shows the warren extending nearer the bank of the Ure than on the 1913 map, owing to construetion of the railway along the river's north bank. In 1894 James Storey moved into Warren House with his family, taking charge of the warren in addition to his role as keeper for the Vyners of Newby Hall, to whom ownership of the warren had passed by marriage. The warren was famous for its valuable breed of silver-greys. Tuke (1794) suggested they were brought from a Lincolnshire warren, having come there from Ireland. Up to 1936 they were being sold to the felt hat industry. Aneedotal account now is that many were sold alive as breeding stock. Whaley (1890) tells of them being sold for coursing. Further back, in 1774 Fothergill records some concern over the possibility of live

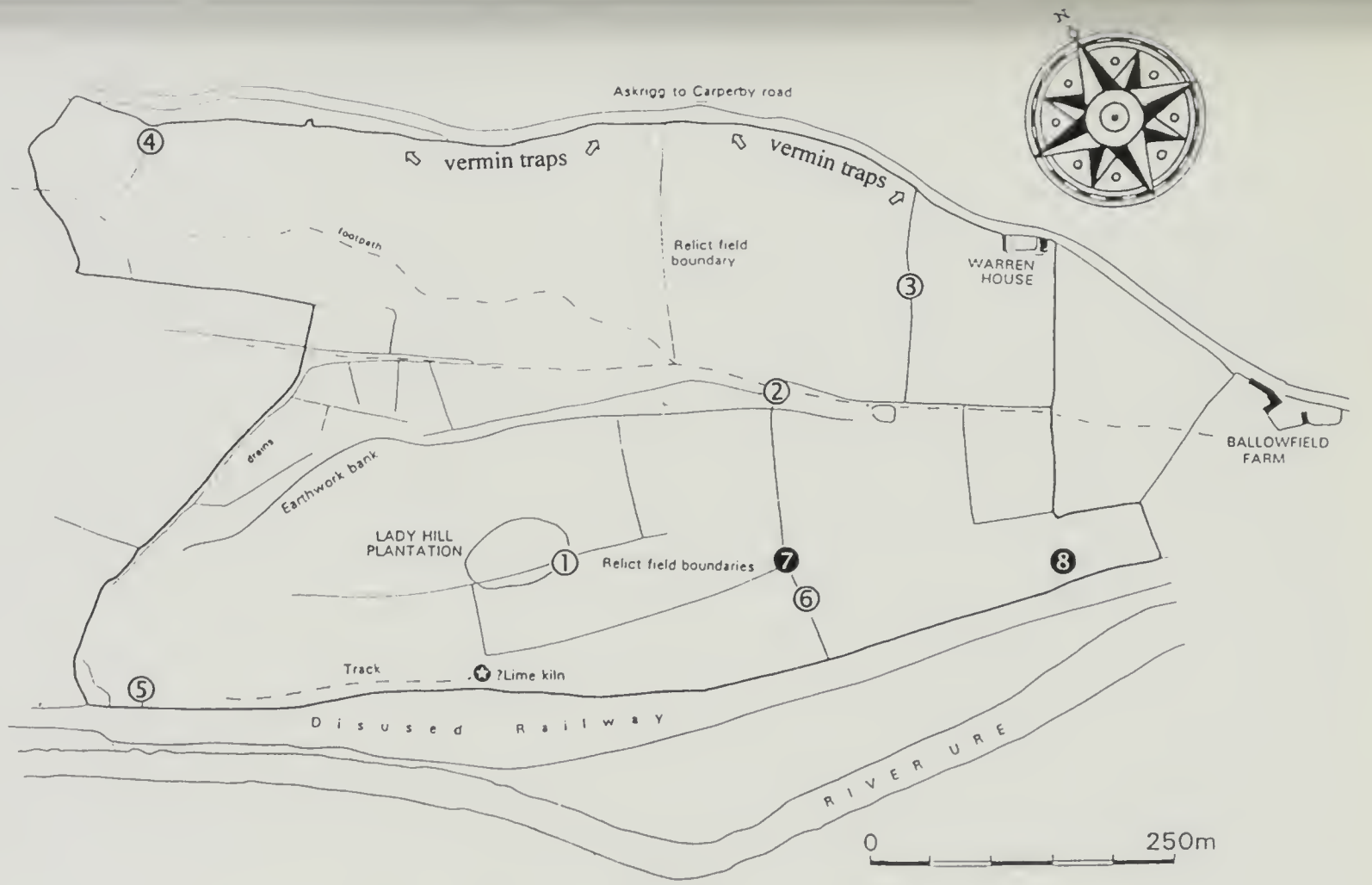

FIGURE 11
Map of Woodhall Warren, North Yorkshire. Based on a map produced for the Yorkshire Dales National Park, and on O.S. of the area. © Crown copyright: ED27433X. Key: 1-6 = rabbit types or tip-traps; 7 and 8 = buildings.

rabbits being sold, and mentions an agreement that this should not be done by the Nappa tenant of that time.

The warren was entirely enclosed by a 6' to 8' high stone boundary wall, its only gate being one down by the warren house. Rabbits were taken either by type or netting. Six types have been located within the warren, immediately by or somewhat subsumed into inner field walls. Both methods of capture would avoid damage to the animals' fur. A distinctive feature of the northern boundary wall is a number of inset alcove-like vermin traps, situated high up along the wall's inner face at intervals. On the flat bases of these alcoves circular traps were placed so that when a marauding fox or stoat attempted to gain exit from the warren, they were attracted by the step-like aperture below the coping. None of the traps used in this specialised situation has been traced as yet, but they are known to have been broadly disc-like and to have been fastened by a metal chain to the mid-reach of the wall below the alcove, so that the victim was often left cruelly dangling. A small enclosure by the eastern boundary wall was used for growing turnips as rabbit-fodder, and these were stored in a small shed in the corner of the field.

Warrening continued after the decline of the very profitable siver-grey industry. Methods of capture changed, however, when intact fur was no longer an overriding priority. Ferreting became acceptable, and snaring replaced the use of the types, which had always been labour-intensive. The Vyners disposed of the estate in 1933, and gave first chance of buying to Robert James Raw, who obtained it for £775. The declining years of warrening activity are fortunately documented in the privately owned diary of Francis Thornborrow Dinsdale (19- -). Between 15 September 1953 and 12 January 1954 he sold 1341 and a half couples of rabbits, when they were selling at 5s 6d each. In April 1955 he notes that the man who bought most of the rabbits paid 4s a couple in February, 3s.6d a couple in March, and only 2s 6d a couple in April. His first record of the advent of myxomatosis into the warren is at the start of that year, 29 January 1955 : 'Found one ---- rabbit in warren home field near henhouse.' Among a few such subsequent entries: '13 March 1955. Saw another rabbit under Stoneman (not in the warren) with m---- (½ ml due n. of warren)'. The last reference of all to the warren is on 2 April 1955: 'Ferreting at west side of big hill at west end of north side. Would not bolt, but got 14 rabbits'.

4. Wharncliffe Chase

Wharncliffe Chase was in mediaeval times an unenclosed chase (Hey, 1975), with free warren granted in 1242. It was enclosed in the 1500s and a lodge was built on the crags in 1510, ultimately with kennels adjoining. From the 16th to mid-19th century deer were the main stock. A charge from the final years of the 16th century (in the rough Latin of the day) against Reginald Thompson, labourer, states that 'he illegally broke into and entered a chase of Richard Wortley and unjustly and illegally without any authority or licence killed and did to death *cervum* in English a deer *tormento* in English with a Gunne'. From 1820 sheep were kept and subsequently became the main concern. The earliest record traced so far of a rabbit-warren on the chase is an area to the east named as 'warrens' on a 1774 map in the Wharncliffe Muniments and under a tenant farmer, Robert Charlesworth. A charming 18th-century map of the chase is uninformative about warrening activity.

Rabbits on the parts of the chase where there is most remaining evidence of warrening were, it appears, primarily bred to provide interesting days hunting and shooting. They and the sheep farmed with them assumed greater importance as deer-chasing declined. Today four areas of the chase hold signs of warrening activity (Fig. 12). The oldest is the earthen boundary embankment of the tenant farmer Robert Charlesworth's 'warrens', already mentioned, to the eastern side of the chase, now known as Warren Plantation and overgrown. The second is a large area to the north of the chase, where there are several pillow mounds which are of distinctive and substantial structure (Fig. 13). Square or rectangular in plan they had sides 10 m or more in length, *c.* 1.5 m in height, revetted in well-dressed stone, and with two or three small muce-holes in the foot or side of each stone face, allowing entry to what appears to have been a two-storey system of stone-and-earth

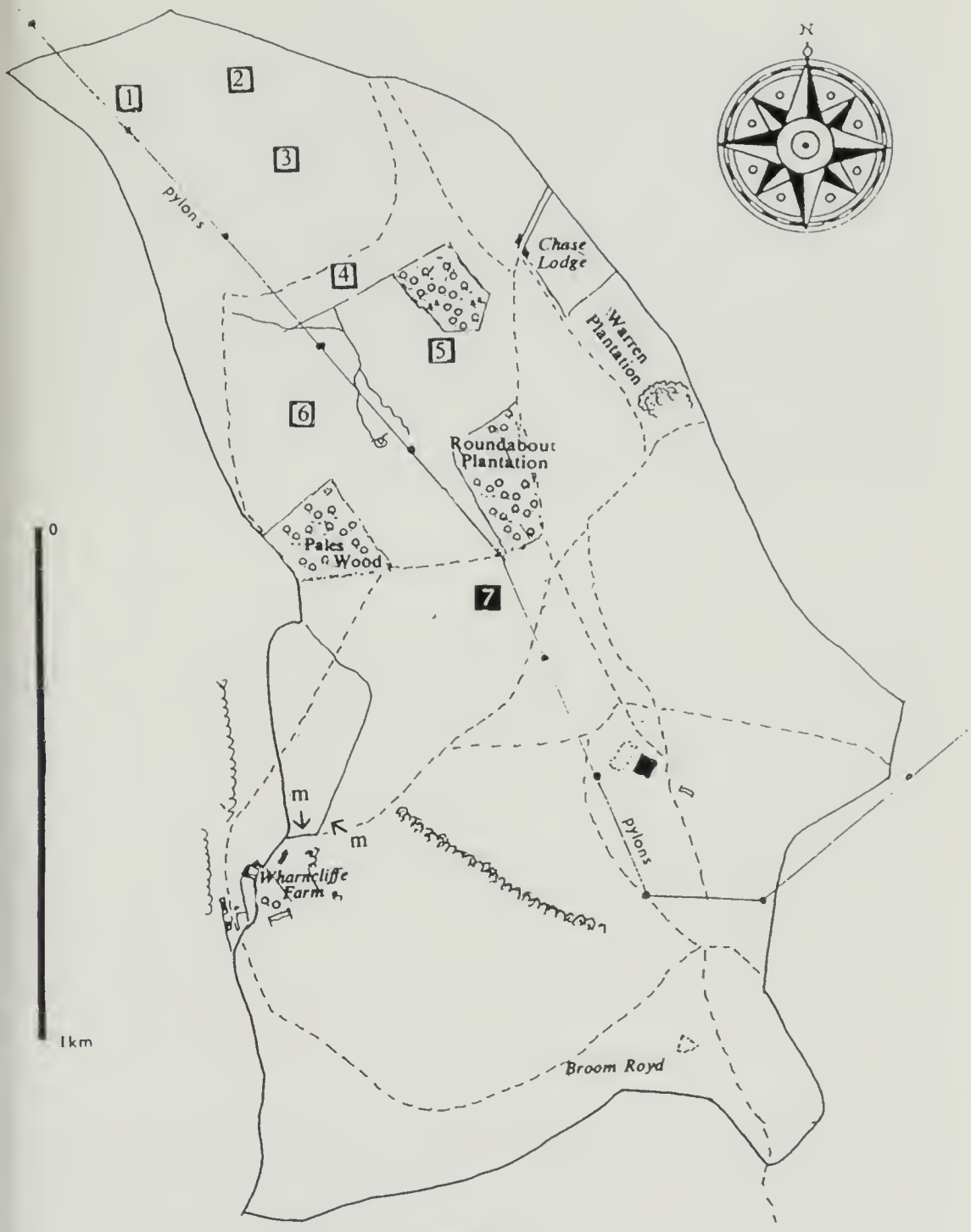

FIGURE 12

Map of Wharncliffe Chase. Based on a map produced by the Ecological Advisory Unit, Sheffield County Council; and on O.S. of the area. © Crown copyright: ED27433X. Key: 1-6 = revetted earth-&-stone pillow mounds (see Fig. 13); 7 = earthen feeding mound; m indicates lengths of wall with muee-gates and muee-holes (see Fig. 14).

FIGURE 13
Remains of revetted pillow mound, Wharncliffe Chase. Photo: A. Henderson.

fashioned burrows within, intended to encourage rabbit habitation and further spontaneous burrowing on the animals' part. The overall capping of each mound was completed by 0.35 m-deep turve-layering. A nearby stretch of the western boundary wall has a well preserved course of shallow flat throughstones projecting on the inner face just below coping level, originally aimed at preventing deer jumping to escape. The third area of rabbiting interest is in the central area of the chase, where there is a large, burrow-pocked, earthen mound *c.* 12 m x 15 m in rectangular plan, which was a feeding mound for rabbits, where turnips, etc, could be laid out as fodder. This mound has lost the surrounding iron rails, *c.* 2 m high, which once protected the rabbits' feed from intrusion by the sheep and any remaining deer on the chase. Lastly, over by the Lodge and towards Wharncliffe Farm is an area where activity was directed mainly at the provision of pleasant days in the field with the gun. Here rabbits were run to and fro for the sportsmen, additional stock being transported from elsewhere on the estate in steel box-traps on shooting days. Remaining evidence of this sport is in the two strategic lengths of field-wall in this neighbourhood which contain, interspaced, four muce-holes (cylindrical pipe-lengths through the base of the wall) and most unusually seven muce-gates (Fig. 14). These are low gates through the wall, typically *c.* 0.9 m wide by 0.45 m high, the wall above them supported by two stout oak beams almost 1 m long and 15 cm square in section. These finely crafted gates show the degree of importance attached to producing a good show of rabbits for the guns.

Conclusion

Since its establishment here as the Normans' coney, *Oryctolagus cuniculus* has moved gradually towards the nearly totally feral existence it enjoys nowadays. Its history here is that of a peculiarly restless ecological entity; more so than in most mammals because of its extreme opportunism, its ecological plasticity and its fecundity. It was brought to these islands as a valuable item, the Normans recognising its desirability not only for the table and clothing, but also as source of profit in home and overseas commerce. Many of the vicissitudes in its history have been closely connected with man. For instance, the establishment of feral colonies by escapees from warrens at the time of the Black Death was favoured by the diminution of custody and husbandry in warren and field. The Agricultural Revolution of the 18th century, with new methods of land fertilization and

FIGURE 14
Muce-gate and muce-hole, Wharncliffe Chase. Photo: A.Henderson.

with winter fodders available, meant more land was rendered arable and stock could be overwintered; by the 19th century there was therefore less demand for the rabbit as food. Encouraged by changes in the game laws, however, feral rabbits quickly began to assume pest proportions. By mid-Victorian times the great commercial warren complexes were in decline; the coney of the Normans had become the British rabbit. Waiting in the wings were the horrors of myxomatosis and haemorrhagial virus.

References

Apicius. *De Re Coquinaria* **2**, 2, 6.
Biadi, F. and Le Gall, A. (1993). *Le Lapin de Garenne*. Hatier.
Bökönyi, S. (1974). *History of Domesticated Mammals in Central and Eastern Europe*. Akademiai Kiado, Budapest.
British Library. Harley. MS 2278 67. v.
Calendar of Close Rolls. Henry III. (1237-1242).
Calendar of Patent Rolls. Edward I (1301-1307).
Catullus. *Carmina* 25, and 37.
Crackles, F. E. (1993). The story of gorse in Holderness. *Holderness Countryside* **39**:12-13.
Cunliffe, B. (1983). *Anatomy of an Iron Age Hillfort*. Batsford, London.
Delort, R. (1978). *Le Commerce des Fourrures en Occident à la Fin du Moyen Age (vers 1300 – vers 1450). Bibliothèque des Écoles Francaises d'Athènes et de Rome* **236**:1-1383.
Dinsdale, F. T. (19--). *Diaries* (privately owned).
East, R. (1891). *Extracts from the Portsmouth Records*. Portsmouth Corporation, Portsmouth.
English, B. (1979). *The Lords of Holderness 1086-1260* (University of Hull Publication). O.U.P., Oxford.
English Heritage. *National Monument 17159. Schedule Entry Jan. 23, 1997.*

Finch, M. E. (1956). The wealth of five Northamptonshire Families 1540-1640. *Northamptonshire Record Society* **19**:1-246.

Flux, J. E. C. (1994). World distribution. In *The European Rabbit* (H. V. Thompson and C. M. King, eds): 8-21. O.U.P., Oxford.

Fothergill, A. (1985). Alexander Fothergill and the Richmond to Lancaster Turnpike Road (M. Hartley. J. Ingilby, D. S. Hall & L. P. Wenham, eds) *North Yorkshire County Record Office Publications* **37**:1-271.

Fothergill, C. (1984). A Diary of Charles Fothergill 1805. *Yorkshire Archaeological Record Series* **142**:1-281.

Fussell, G. E. (1955.) The coney warren a century ago. *Yorkshire Life Illustrated* (Jan, 1955): 31.

Gilbert, J. M. (1979). *Hunting and Hunting Reserves in Medieval Scotland.* John Donald, Edinburgh.

Harris, A. (1990). The rabbit warrens of East Yorkshire in the 18th and 19th centuries. *Yorkshire Archaeological Journal* **62**:429-443.

Harris, A. and Spratt, D. A. (1989). Rabbit warrens on the Tabular Hills: archive of field and documentary work 1987-1988. W.Y.A.S. MS1523.

Harris, A. and Spratt, D. A. (1991). The rabbit warrens of the Tabular Hills, North Yorkshire. *Yorkshire Archaeological Journal* **63**: 177-206.

Hayes, R. J. (1965). *Manuscript Sources for the History of the Irish Civilisation.* G. K. Hall, Boston.

Haynes, R. G. (1970). Vermin traps and rabbit warrens on Dartmoor. *Post Medieval Archaeology* **4**: 147-164.

Henderson, A. (1979). Pompocali, a topographic curiosity. *Naturalist* **104**: 75-87.

Hey, D. (1975). *The Making of Modern Yorkshire.* South Yorkshire County Council, Sheffield.

Hirons, M. J. D. (1994). The flora of the Farne Islands. *Transactions of the Natural History Society of Northumbria* **57**: 69-114.

Hurrell, H. G. (1979). The little-known rabbit. *Countryside* **23**: 501- 504.

Hyland, P. (1978). *Purbeck, the Ingrained Island.* Gollancz, London.

Lawson-Tancred, T. (1937). *Records of a Yorkshire Manor.* Edward Arnold, London.

Minshull, J. (17--). Sunderlandwick: Notice of John Minshull. Held in the East Riding of Yorkshire Archives Office, Beverley. DDGR 20/1.

Moorhouse, S. (1991). Norton Tower, Rylestone, North Yorkshire. *C.B.A. Forum 1991. Annual Newsletter of the CBA Group 4.*

Morton, W. (1954). The Book of William Morton, Almoner of Peterborough Monastery 1448-1467. *Publications of the Northamptonshire Record Society* **16**.

Oxford, M. J. (1986). *Planning for Conservation of Wildlife and Archaeological Features on a Nature Reserve in Britain.* M.Sc Thesis, University of Calgary, Alberta.

Pliny the Elder. *Natural History* **8**: 217; 226.

Sheffield City Archives (1774). A Map of Wharncliffe Moors. *Wharncliffe Muniments TAN 3L.*

Raine, J. (1852). *The History and Antiquities of North Durham.* J. Bowyer Nichols, London.

Spratt, D. A. (1989). *Linear Earthworks of the Tabular Hills, North-east Yorkshire.* J. R. Collis Publications, Department of Archaeology and Prehistory, University of Sheffield, Sheffield.

Strabo. *Geography* **3**, 2, 6; **3**, 5, 2.

Stuart, A. J. (1982). *Pleistocene vertebrates in the British Isles.* Longman, London.

Tuke, J. (1794). *General View of the Agriculture of the North Riding of Yorkshire.* Board of Agriculture, London.

Turton, R. B. (1894). The Honor and Forest of Pickering. *North Riding Records. New Series* **1**:1-280.

Varro. *Rerum Rusticarum* **3**, 12, 6-7.

Warner, G. F. (1912). *Queen Mary's Psalter.* Brotherton Library, Leeds. Special Collections Art E-8q. Royal MS 2B VII in B.M.

Whaley, C. (1890). *Parish of Askrigg.* Skeffington, London.

Williams, S. W. (1895). Tiles found at the restoration of Bangor cathedral. *Archaeologia Cambrensis [5th Series]* **11**:107-111.

Williamson, T. and Loveday, R. (1988). Rabbits or ritual? Artificial warrens and the Neolithic long mound tradition. *Archaeological Journal* **145**: 290-313.

Winch, N. J. (1822). Remarks on the geology of Lindisfarne or Holy Island. *Annals of Philosophy* (December **1822**): 169.

Woods, E. C. and Brown, F. C. (1960). *The Rise and Progress of Wallasey* 2nd edition. Wallasey Corporation, Wallasey.

Yorkshire Dales National Park (1996) *Woodhall Rabbit Warren, Carperby, North Yorkshire. Archaeological Survey (E. Denison).*

Zeuner, F. E. (1963). *A History of Domesticated Animals.* Heinemann, London.

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THE HORSE-TROUGH OSTRACOD *HETEROCYPRIS INCONGRUENS*

GEOFFREY FRYER

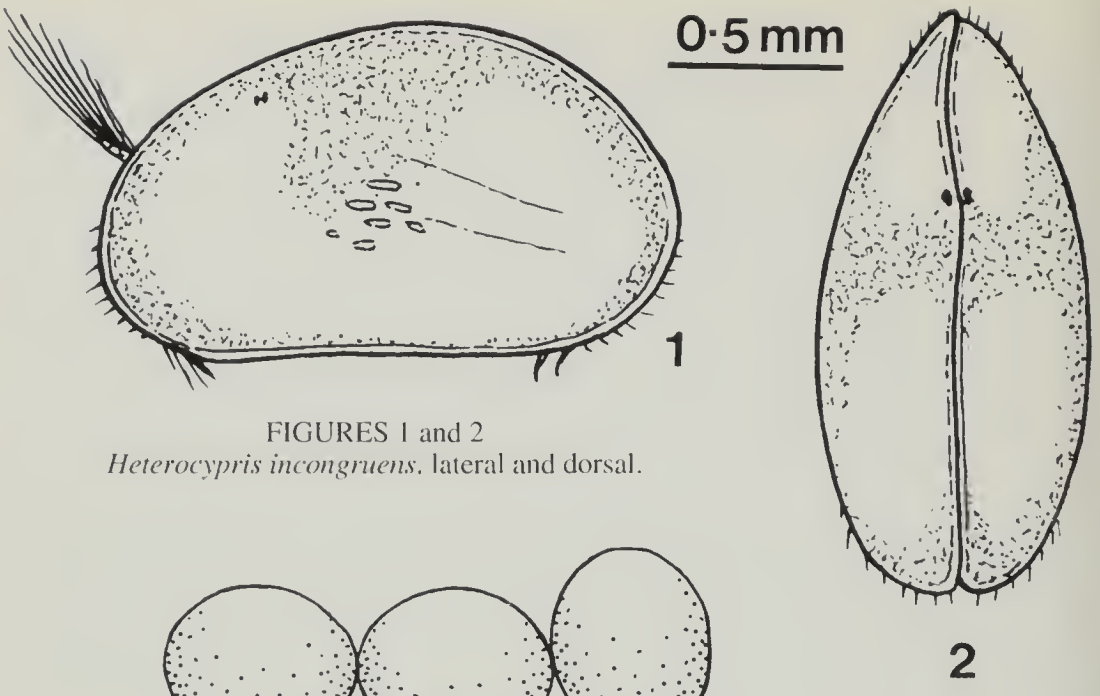
Institute of Environmental & Natural Sciences, Lancaster University, Lancaster LA1 4YQ

INTRODUCTION

The freshwater ostracod *Heterocypris incongruens* (Ramdohr) (= *Cyprinotus incongruens*), a minute bivalved crustacean, has an apparently almost cosmopolitan distribution. It is common in Britain and elsewhere in Europe. Ecologically tolerant, it favours small water bodies of various kinds and has such a liking for horse-troughs and similar receptacles – a liking seldom shared by other ostracods – that it merits the common name of the horse-trough ostracod. Such a designation may serve to draw attention to this interesting crustacean, to some of the phenomena that it displays, and to the intriguing problems that it poses.

THE ANIMAL AND ITS LIFESTYLE

Only females (Figs. 1 and 2), are known in Britain, where reproduction is entirely parthenogenetic. They may attain a length of about 1.8 mm but are frequently smaller. Yellowish in colour, they often become dark reddish brown dorsally as they get older. The ovaries lie between the inner and outer lamellae of the carapace on each side and contain orange eggs that can be dimly seen through the chitinous outer lamella. The surface of the carapace ('shell') is smooth and polished. *H. incongruens* is an active animal that can swim briskly by means of its antennules and antennae which can be extended outside the carapace and are provided with long natatory setae ('swimming bristles'). It can also crawl by use of the antennae and first pair of thoracic limbs, both of which terminate in stout claws. As a means of defence it can bring together the valves of its carapace and shut itself



FIGURES 1 and 2
Heterocypris incongruens, lateral and dorsal.

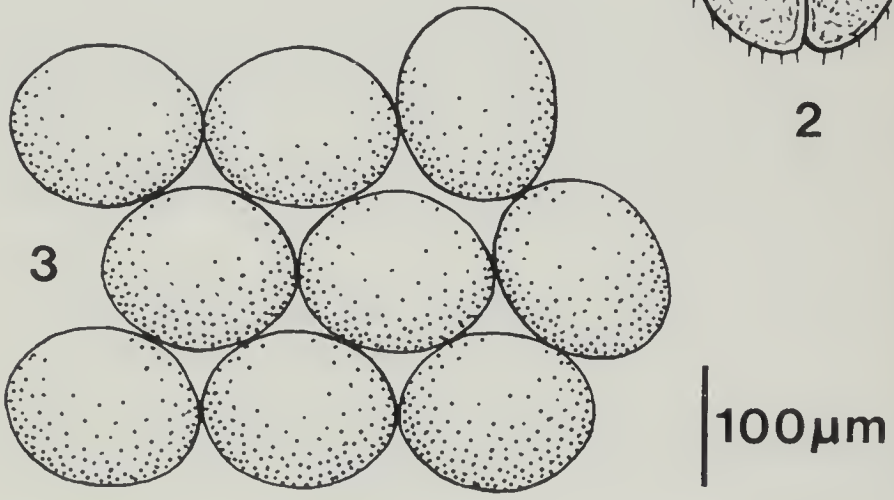


FIGURE 3
Part of a cluster of eggs.

within like a tiny mussel. An omnivore, it can subsist on algae and organic detritus and can also skeletonize leaves by rasping their soft cells – lettuee leaves are rapidly degraded if a large population is at work. It exploits windfalls of dead animal matter, and when it ean seize them, whieh it is not particularly well equipped to do, it kills and devours such small animals as *Daphnia*.

Like many freshwater ostraeods, but unlike most crustaceans, it attaches its bright orange eggs to firm substrata, sueh as a pieee of rotting wood, a dead leaf, or stone surface. This applies to all eggs save the first bateh produced, which are (always?) attached to the carapaee and east off at the final moult, and to a few that may be shed free. The subspherical eggs (Fig. 3), whieh have a tough, proteetive outer pellicle and two inner membranes, are mostly deposited in elusters, often in parallel rows. A lifetime's production may be up to at least 100 eggs, laid in small batches, but not all individuals are so productive. Several animals often lay eggs in close proximity and veritable crusts of eggs ean then be seen with the naked eye. These are usually one layer deep, but overlaying sometimes occurs. Veins are attractive when dead leaves are used, and when only these veins remain they often bear 'ropes' of eggs.

An egg hatches as a minute nauplius, the basic crustacean larva, hidden by a bivalved shield. This has led to erroneous statements that ostracods are born as 'juveniles' not

larvae. After passing through 8 larval and pre-adult stages, adulthood is reached, which, depending on temperature, takes between about 5 weeks and 5 months. Egg laying begins with the eighth moult. Adults may survive for several months.

An inordinate fondness for horse-troughs

A preference for horse-troughs and similar receptacles is a noteworthy and well-known feature of the ecology of *H. incongruens*. For example, although such troughs were not specifically sought during a survey of the freshwater Crustacea of Yorkshire, it was found in six, scattered over a wide area and, atypically, in a spring-fed metal trough supporting a growth of charophytes (Fryer, 1993). Ostracods found in a wooden tub when I was a small boy were certainly this species, which I have encountered in similar troughs elsewhere in England, e.g. in Cumbria, Cheshire and Gloucestershire. Troughs are often, but not always, turbid, green with algae, contain dead leaves or other decaying organic matter, are sometimes foul, and must often suffer from oxygen deficiency. Indeed, Fox and Taylor (1955) demonstrated that *H. incongruens* can not only flourish at low oxygen concentrations but that it prefers such conditions to well aerated water. Green (1959) showed it to be well adapted to situations low in oxygen and even to be able to endure anaerobic conditions for at least two weeks, and to lay eggs while so doing; he also found that it produces a yellow pteridine pigment which he suggested may play a part in intermediate metabolism under anaerobic conditions. Nevertheless, individuals often congregate near the surface, where oxygen is most plentiful, and lay many of their eggs there.

Conditions differ much in different troughs. In Cumbria I have found *H. incongruens* at Witherslack, on the Carboniferous limestone, in a trough made from limestone blocks, somewhat less than 3 m^2 in area and up to almost half a metre deep when full. This is clearly alkaline, is usually green with suspended algae, often foul, and newts breed in it. Different conditions prevail in a smaller, glazed ceramic horse-trough near Lazonby that intermittently receives clear water from sedimentary Permian rocks. Different again is a garden trough at Grasmere, less than 0.5 m^2 in area, of local volcanic rock, containing clear, perhaps slightly acidic, water. However, like most ostracods, *H. incongruens* shuns very acidic water, perhaps because of the difficulty of finding enough calcium with which to impregnate its carapace rather than avoidance of acidity as such. It was not seen in the Southern Pennines during an exploration of stone troughs that receive cold springs. These are modified rheocrenes, sometimes have a carpet of bryophytes, and harbour a variety of cold-loving micro-crustaceans. Here it may be deterred by cold, acidity, low calcium levels, well oxygenated water, or a combination of these factors. It has, however, been recorded in springs in Europe (see Klie (1938) for summary) though these are perhaps largely limnocrenes (seepages), where the water spreads out and may quickly warm up after leaving the ground. Indeed, this is precisely how Bronshtein (1947) describes its occurrence in limnocrenes, where he specifically states that it lives 'far from the outlet of the spring, and also well heated'. The spring-fed Yorkshire trough is an unexplained exception.

A liking for horse-troughs and similar habitats is shown by finds in the Channel Islands, themselves isolated and not easy for freshwater animals to find. In Guernsey, I found it in small stone troughs at St. Peter Port and Saumarez. Even more striking, on the much smaller island of Sark I found it in three such troughs, one very small and containing only a few centimetres of water and, as troughs unfortunately now often do, much rubbish. Most remarkable of all, *H. incongruens* has been found on the small, remote Easter Island in the Pacific Ocean (Dumont & Martens, 1996), being one of only 5 micro-crustaceans found there, of which 2, possibly 3, of the others are suspected to be introductions. Of the several sites in which it was found, one was 'a stone basin' near the shore, another 'a eutrophic stone basin used for watering horses'! How *H. incongruens* locates such sites is a mystery to be considered. It has also been recorded in water-filled tree holes (Klie, 1938).

H. incongruens also occurs in what might be regarded as natural equivalents of horse-troughs. In Northern Manitoba, Canada, it is common in rock pools that occupy small

depressions on quartzite bluffs. Of 157 sampled pools of mean area about 1 m^2, it was found in 67 (Havel *et al.*, 1990). Likewise Ganning (1971) described a rock pool in Sweden which supported a persistent population of *H. incongruens* as 'a very typical biotope' for this species. This had a maximum volume of about 300 litres and often dried up completely. Other sites are extremely diverse but seemingly always small, except perhaps shallow rice-fields. Ponds and pools, including foul and turbid farm ponds, ditches and muddy seepages are the sort of places favoured.

Eggs for all occasions

In Britain all eggs are produced parthenogenetically. No male has ever been recorded and this is so for much of Europe, Northern Asia and N. America, although males do occur sporadically in Europe and have been found in N. and W. Africa and Palestine. It is sometimes suggested that males become more prevalent in warm, southern latitudes, but more evidence is needed. No males have been seen in Italian ricefields, where much work has been done, but they are known from further north in Germany, Hungary and Poland. Because they are produced by ameiotic parthenogenesis, (i.e. without any reduction of the chromosome number from the diploid condition), and no genes are received from a male, every egg has the same genetic constitution as its mother and all eggs produced by a given individual are genetically identical. Nevertheless, even under the same conditions, eggs of a single batch do not all behave alike. (Even genetically identical eggs may respond in different ways to different conditions). Depending on temperature, many hatch within as little as 3 to about 14 days. Others do so after a longer time interval. As this period is very variable, it is not easy to define the types of eggs. By hatching within, to set arbitrary limits, say 14 days, eggs reveal themselves as immediate developers. When they take longer, they may be said to have entered a period of rest or diapause. However, among these some may hatch within say 15 to 150 days, while others may become dry, in which condition they can withstand desiccation and, like plant seeds, remain dormant for long periods. These long-lived eggs are here referred to as dry resting eggs. In this condition they are exceedingly resistant, as indeed are wet eggs, the latter, and presumably the former, being able to withstand even freeze drying.

Sohn and Kornicker (1979) froze wet eggs for several days at *c.* –25°C, then freeze dried them at –25 to –30°C in a 0.01 millibar near-vacuum for several more days. In one case eggs were kept for a day in a near-vacuum of 0.001 mb. Such temperatures are similar to those that previl at altitudes of about 6 km, the pressures like those at 80 to 100 km. As wet eggs were used, dehydration must have been rapid and very rigorous. On immersion in water, many eggs hatched (37% of those subjected to the greatest reduction in pressure did so) and grew into adults, which produced viable eggs. Freeze drying dehydrates tissues very effectively. Ability to survive this process is interesting as it is apparently by driving out the last trace of water that the very heat-resistant eggs of the notostracan branchiopod *Triops granarius* can be destroyed (Carlisle, 1968).

Resting eggs of freshwater calanoid copepods that become buried in lake sediments can apparently remain viable for more than 300 years (Hairston *et al.*, 1995), and those of some species of *Daphnia* may be able to do so for 125 years (Cáceres, 1997). However, even if viable, such eggs are so deeply buried that their chance of hatching is exceedingly remote. Whether dried eggs of *H. incongruens* can survive so long remains to be explored, but some ostracod eggs have survived for up to 30 years. Wet diapausing eggs of *H. incongruens* appear to be less long-lived than dry resting eggs and their role seems generally to be to tide the population over one period of adverse conditions, e.g. wintertime in Britain, but more information is needed.

That *H. incongruens* produces both quick-hatching and resting eggs by parthenogenesis is in itself interesting because in many small freshwater crustaceans e.g. branchiopods such as *Daphnia* and its allies, and fairy shrimps, resting eggs are usually (but not invariably) produced from sexual (fertilized) eggs. Furthermore, the production of quick-hatching parthenogenetic, and resting fertilized eggs usually involves different underlying genetic

and cytological mechanisms. In *Daphnia* for example, parthenogenetic eggs, which have the same number of chromosomes as the mother, are carried in the latter's brood pouch and there hatch quickly, being liberated as free-swimming juveniles. Production of sexual eggs on the other hand involves a halving of the number of chromosomes during the making of the egg, with fertilization by a male sperm (whose chromosome complement is half that of the male) restoring that number to the usual (diploid) condition. The fertilized resting eggs, just two in this instance, are placed in a protective receptacle formed from the carapace which is then cast off by the female and goes by the name of an ephippium. In *H. incongruens* there is no such clear distinction between the production of the two kinds of eggs, and a female can lay a mixture of quick-hatching and resting eggs. This remarkable ability has not attracted the attention it deserves, and the mechanism whereby it achieves this feat remains mysterious. The possibility that eggs react in these different ways according to prevailing conditions can be ruled out by the fact that some eggs of a batch may hatch quickly while others, from the same batch, may enter a period of dormancy. Experiments to sort out these problems face the difficulty that all eggs look alike. They can only be classified after the event on the basis of their performance. In some freshwater crustaceans, eggs that develop quickly have coarse-grained yolk and vacuoles are present, while drought-resistant resting eggs have fine-grained yolk and no vacuoles. Whether this applies to *H. incongruens* remains to be investigated, but it seems unlikely as females would have to produce eggs of two kinds, sometimes as components of a single laying. Like those of other crustacean resting eggs, those destined to enter diapause (i.e. to 'rest') develop to at least the gastrula stage or a little beyond. Eggs exposed to the air immediately after laying will presumably perish if they have not reached this stage.

It is difficult to draw a clear distinction between immediately hatching and resting eggs in *H. incongruens*. Thus, Angell and Hancock (1989) isolated 48 females, one per container, and put each egg laid into a separate container. Of 2,662 eggs so isolated, 842 (32%) hatched within 125 days. Of these, 309 hatched within 5 days and 88 more in the next 5 days. In the third 5 day period only 15 eggs hatched and a rather similar hatch rate continued up to about 60 days, then increased until, in the period between 76 and 80 days, 48 eggs hatched. The hatch rate then declined steadily and hatching had virtually ceased when observations ended after 125 days. The remaining 68% of the eggs laid were potentially resting eggs or had died.

Because the parentage of each egg was known it was possible to see how many eggs from a particular female hatched within the first 10 days and how many did so within 125 days. There was enormous variation. For example, of the 99 eggs produced by the most fecund female, 43 hatched within 10 days while none of the 83 eggs of another individual did so. The position in the sequence of laying bears no relationship to the type of egg. There is no apparent pattern: a female may produce diapausing eggs anywhere within the sequence – or lay only such eggs. Eggs may be deposited at a steady rate, or in bursts of activity. Whether any of the variability in egg behaviour can be explained by the fact that the animals used belonged to different clones (see below) is not known. Certainly, however, such remarkable behaviour as both rapid and slow hatching of eggs in a single batch cannot be so explained.

These observations incidentally revealed great variation in fecundity – from 99 to 3 eggs in this batch of 48 females. The animal that laid 99 eggs survived for 34 days after laying began; the next most productive (96 eggs) for 61 days. The 3-egg female lived for 40 days after laying its last egg but its life span is not recorded.

Parthenogenesis and clonal diversity

As all eggs, at least in Britain (and in most populations elsewhere), are produced by ameiotic parthenogenesis, the offspring to which they give rise are genetically identical to their mother. Long-held theoretical opinion has it that little genetic diversity is therefore to be expected. Furthermore, deleterious mutations gradually accumulate in asexual lineages because individuals with the fewest such mutations are, in the long term, liable to be lost

by chance, with an inevitable decline in fitness, or so the theory goes. Indeed, Lynch (1984) demonstrated a rapid decline in genetic variation in *Daphnia* during periods of parthenogenetic reproduction, and Spitze (1991), working with a population of *D. pulex* in which there is an alternation between periods of parthenogenesis and sexual reproduction, showed that between 93 and 99% of the initial genetic variation can be lost in the course of a season of parthenogenesis spanning 8 to 10 generations. These losses are made up during the annual bout of sexual reproduction. This cannot happen in permanently parthenogenetic populations of *H. incongruens*, yet such populations persist and are widely distributed. To this we shall return.

Because of the drawbacks associated with parthenogenesis it has been argued that asexual species are less well endowed for long term survival than sexually reproducing species. The latter generate enormous variability through repeated mating and the inheritence of genetic material from two parents, no two of which, save monozygotic twins, are alike. This means that genotypes of many kinds are available to cope with environmental diversity, and selection for the fittest genotypes can occur. Historical evidence in support of this view has been adduced from just one group of animals – freshwater ostracods. Their calcite-impregnated carapaces preserve well in alkaline situations, and the patterns of such remains deposited at several Holocene sites in Britain and Europe between *c.*10,000 and 5,000B.P. – a period of considerable climatic change – suggested that sexually reproducing forms had an advantage over those reproducing asexually, and that the advantages of asexuality are generally short-term (Griffiths & Butlin, 1995). Nevertheless, the idea that obligate parthenogenesis leads, literally, to a dead end can be challenged. Bdelloid rotifers, of which there are many species, all apparently entirely parthenogenetic, have evidently existed for long periods. The same is possibly true of a group of freshwater ostracods, the Darwinuloidea, that brood their young and whose swollen brood pouch can be seen in fossils, of which there is a record of females only that extends over at least 70 million years. However, an alleged male of the extant *Darwinula stevensoni* has been described which, if correct, is an embarrassment to an otherwise fascinating story, though such rare males are regarded by Rossetti and Martens (1996) as examples of non-functional atavisms ('throwbacks' to a former state) of little or no significance in reproductive strategies.

More certain is that the theoretical belief that parthenogenetic animals show little variability is in some cases erroneous. The technique of enzyme electrophoresis has shown that there are many different clones of *H. incongruens*. The first to demonstrate such clones in this, and indeed in any ostracod, were Sywula and Lorenc (1982). Electrophoresis reveals some of the genetic variation of an organism in the form of bands on a gel, whose pattern is the same in all individuals of a single clone, but different in different clones. The bands reveal the genotype of an individual at several, but by no means all, its enzyme loci. Clones revealed in this way are sometimes referred to as electrophoretic clones. When patterns differ at several loci their possessors are termed multilocus genotypes. They are morphologically identical, or at least this seems to be the case though there is no theoretical reason why a difference, which would probably be small, should not be morphological.

Electrophoresis can only reveal differences in enzyme loci for which tests are possible: other such differences probably exist. The technique may therefore not detect all the clones that are present in a given species or population. The only example known to me of clones of ostracods that can be distinguished by simple inspection concerns what in Britain is the exclusively parthenogenetic *Psychrodromus olivaceus* which is usually green in colour but of which I found populations in two separate springs in Yorkshire that included both green and white individuals (Fryer, 1993). Presumably the differences between clones include perhaps a single gene for colour whose effects are seen in this striking way rather than as hidden differences revealed by electrophoresis. It is of course possible that both green and white clones each embrace several electrophoretic clones.

In spite of theory, *H. incongruens* has at its disposal a degree of genetic variation. Moreover, several clones sometimes co-exist. This increases the chances of survival or of

building up large populations because conditions deleterious to one clone may be less so, or even advantageous, to a different clone. That this is no mere hypothetical argument has been convincingly demonstrated in Italian ricefields. Here obligate parthenogenetic populations of *H. incongruens* flourish. No males have ever been found there. Italian ricefields are flooded from May to September. During the rest of the year small puddles a few centimetres deep remain. Early investigations revealed 5 clones. Although the situation later proved to be more complicated than at first thought, it is convenient initially to ignore later findings and refer to the original work, which remains valid. Of the 5 clones, each of the 3 commonest favours, or flourishes best at, a particular temperature and have been designated as winter, summer and intermediate clones. To simplify the story attention is concentrated largely on the winter and summer clones.

In the early part of the year, the winter clone predominates or exists alone and the summer clone is completely unrepresented. A few individuals of this clone appear in May and by the end of July it has entirely replaced the winter clone (Rossi & Menozzi, 1990). Experiments confirm the adaptive differences between clones. Individuals of the various clones reared at different temperatures differ strikingly in performance at extreme temperatures. At 4°C only individuals of the winter clone survive: those of the summer clone die within a few days. Those of the intermediate clone survive a little longer. At high temperatures the advantage changes in favour of the summer clone, and at 32°C individuals of the winter and intermediate clones die in a few days while those of the summer clone may survive for up to 60 days. (Life spans are in any case shorter at high temperatures). Tested at 16°, 24°, 28° and 32°C, members of the winter clone laid most eggs at the lowest temperature and very few at the highest, while the summer clone did the reverse, laying scarcely any eggs at 16°, and most at 32°C. The intermediate clone laid most eggs at 24°C. Likewise eggs of the winter clone hatched much better at 16°C than did those of the summer clone: at 32°C the position was reversed. Of eggs laid by the winter clone, the percentage of diapausing eggs rose rapidly at high temperatures (such eggs are an insurance against adverse conditions) but fell in the summer clone. It is therefore clear that the summer and winter clones of *H. incongruens* are adapted to life at the warm and cooler temperatures at which, respectively, they occur in nature.

As detailed investigations by Carvalho (1987, 1988) had revealed seasonal electrophoretic clones in an almost entirely parthenogenetic population of the anomopod 'cladoceran' *Daphnia magna*, the situation in *H. incongruens* is probably typical of parthenogenetic crustaceans, and perhaps of parthenogenetic invertebrates in general. The work on *Daphnia* not only revealed a seasonal succession of clones but showed that their survival and ability to flourish were clearly related to the temperatures at which they occur in nature, and that egg production of different clones was also geared to appropriate temperatures. This last point, which also applies to *H. incongruens*, is important, as egg production had long been thought to be related in a simple manner to such environmental factors as food levels and temperature (which are of course important) and not to genotype (i.e. not to the genetic attributes of their producer). In fact, for some clones a rise in temperature results in a decline in egg production (though it rises in other clones) and not an increase, as was generally assumed to be the case. This is so also in *H. incongruens* (Rossi *et al.*, 1991).

Although no morphological differences have been found to be associated with electrophoretic patterns, Rossi and Menozzi (1990) found that while individuals of the winter clone had a mean length of 1.55 mm, in the summer clone it was only 1.15 mm. This is not surprising, as small crustaceans that develop at high temperatures tend to be markedly smaller than those that do so in cooler conditions (in Ghana females assigned to *H. incongruens* by Benzie (1984) had a length of between 0.8 and 0.93 mm), and this appears to be a purely phenotypic effect; for example, Coker (1933) found that individuals of the copepod *Acanthocyclops vernalis* reared at 7-10°C are 'invariably so much larger' than those reared at 18-19°C, and 28-30°C that the difference is obvious to the naked eye. It is therefore surprising that Rossi and Menozzi (1990) say that significant size differences

between the clones persisted through at least three generations reared at *c.* 20-24°C, which suggests that the differences have a genetic basis. However, reared individuals of the winter clone had a mean length of 1.26 mm, which is considerably less than in the field, and consistent with development at higher than winter field temperatures. Had size determination been entirely genetic these animals would have been the same size as their parent. The summer clone had a mean length of 1.04 mm, again less than the field population, but in this case, perhaps unexpected, as summer temperatures are sometimes higher than those at which these individuals were reared. Again, however, an environmental factor is clearly involved. Nevertheless, individuals of the winter clone were still larger than those of the summer clone, which supports the likelihood of a genetic effect, though the disparity was less than in the field. The general diminution in size of the reared animals may in part be a result of keeping them in very small volumes (20 ml) of water. It seems best to keep an open mind on this matter. While the rearing experiments suggest that there may be a genetic element in the size difference between summer and winter clones, they do not take into account what seems to be a general phenotypic effect of temperature on size.

Temperature is not the only thing that changes seasonally in temperate climates. Day-length does likewise and is used as a cue for changes in reproductive behaviour by several small crustaceans. In some species of *Daphnia* short day-length plays a key role in inducing a change from parthenogenetic reproduction to the production of ephippia (resting eggs) and the males that are usually required to fertilize them. Shortening day-length also serves as a cue leading to the production of resting eggs in certain copepods. However, *H. incongruens* seems to be the only ostracod for which information has been obtained on the effect of day-length on reproductive behaviour. Using summer and winter clones from Italian ricefields, Rossi and Menozzi (1993) showed that, when kept at 24°C in a regime of 16h light and 8h dark, individuals of the summer clone survived longer and produced more eggs than those of the winter clone, which accords with their occurrence at a time of the year with long days. When kept at 24°C in 12h each of light and dark there was no significant difference in the survival of the two clones. However, of the eggs produced by the winter clone, the percentage of diapausing eggs was greater, as was the actual production of such eggs, than it was in the summer clone. Resting eggs are often produced by small crustaceans as a response to unfavourable conditions (though these are not always easy to define). Long days are favourable to the summer clone, but unfavourable to the winter clone, so the reaction is 'sensible' even if the mechanism is not understood. We may here, however, have a possible clue to the factors that regulate the production of diapausing eggs in this ostracod, though it does not explain everything concerned with what is still a mysterious matter.

Work on *Daphnia* provides supporting clues. Carvalho and Hughes (1983) showed that two populations of *D. magna*, from different ponds, and evidently of different clones, kept at the same density of individuals, at the same temperature, and given identical amounts of food, nevertheless differed in the incidence of ephippium production over a range of what were known to be inductive photoperiods. Other experiments also suggested that ephippium production may be triggered by subtle differences in day-length in different clones in a single pond.

By extending the investigation of clones to another ricefield many kilometres further up the Po Valley, many more clones of *H. incongruens* were found. Indeed, although sampling was less intense than at the first site, 26 multi-locus genotypes were found (Rossi *et al.*, 1993) and further work increased the number to 35 (Rossi *et al.*, 1996). This difference in clonal richness of the two populations is considered later. These clones also exhibit seasonal patterns. However, instead of one clone dominating a particular season, a cluster of clones do so, to be replaced by other clusters at other times of the year. Nevertheless, clones with the same seasonal cycle, e .g. summer clones, may employ different strategies. Thus one summer clone produces almost entirely eggs that enter a period of diapause while another produces only a small percentage of such eggs. This makes one wonder if the

animals used by Angell and Hancock (1989), that behaved in different ways in this respect, may have belonged to different clones. Such differences endow a species with the ability to cope with a variety of environmental conditions, which is advantageous in the often ephemeral habitats frequented by *H. incongnens*. They may go some way towards explaining the statement of Angell and Hancock that 'no environmental stimulus is needed to induce the production of dormant eggs' and that these form a normal part of the output of every female even though conditions at the time of laying are suitable for immediate hatching. Problems, however, remain. If no cues that stimulate the production of diapausing eggs are involved, it is possible that the production of both kinds of eggs by all clones allows clonal succession to take place simply by crude climatic elimination of inappropriate seasonal clones. As we have seen, however, there is some evidence that cues are used, e.g. a long day-length appears to induce the production of diapausing eggs in winter clones.

Likewise, while it seems logical to deduce from the incidence of seasonal clones that their diapausing eggs hatch at the appropriate time of the year in response to particular stimuli, Angell and Hancock maintain that 'no special environmental stimulus is needed' to induce hatching save that conditions are 'favourable for development'. Again one can envisage inevitable hatching and climatic elimination of inappropriate clones, though the enormous variability of hatching makes it difficult to see how any mechanism, such as a day-degree effect, might operate. The observations of Angell and Hancock were not designed to answer such questions nor carried out under conditions suitable for this. In fact, Rossi *et al.* (1991) showed that both wet diapausing and dry resting eggs of summer and winter clones of *H. incongruens* differed in their response to conditions at the time of hatching. Eggs from both clones were obtained from individuals kept at 28° and 32°C (which happened to provide abundant material), subjected to the same treatments of light: dark regimes and temperatures, and then tested for hatching abilities at 32° and 4°C. In all cases eggs from the winter clone hatched more quickly and in greater numbers than did those of the summer clone (which in some cases failed to hatch within the time span of the experiments). Thus different responses to hatching stimuli in long-lived eggs of summer and winter clones are indicated, but how these are to be interpreted remains problematic. Indeed, it is mysterious why eggs of the winter clone should hatch at high temperatures. That those used were laid by females kept at high temperatures, at which they survive badly, may complicate an already complicated situation. It is also possible that in northern areas, where *H. incongruens* over-winters either as wet diapausing or dry resting eggs, cues for hatching may be more simple than in populations where a series of clones replace each other throughout the year.

Enzyme electrophoresis has also revealed clones of *H. incongruens* in Canada. Seven such were found in populations living in tiny rock pools in Manitoba. Of 42 investigated pools, 31 revealed only one clone, 10 pools each held 2 clones and one had 3 (Havel *et al.*, 1990). These pools often lie in close proximity, which may facilitate dispersal. In Italy, in each of five small temporary ponds only one clone was detected (Rossi *et al.*, 1993). No assessment of the number of clones present in a single horse-trough has been made, but most such populations probably consist of a single clone. The chance of a trough being colonised more than once is even lower than is that for a single such event. Such sites could however, receive more than one clone if a leaf or other object derived from a larger habitat were to arrive carrying a clump of eggs deposited by more than one female that belonged to different clones.

How clonal diversity has been achieved

Parthenogenesis is clearly derived from sexual reproduction and has arisen many times among ostracods. The existence of numerous parthenogenetic freshwater species, and the obvious success of some of them, suggests that the alleged drawbacks of parthenogenesis, namely an inability quickly to generate genotypic diversity, has been successfully overcome by exploiting numerous clones. How has this clonal diversity arisen? Some of it

has undoubtedly done so by mutation within asexual lineages, though genetic work suggests that mutation rates are not abnormally high. Some of it also seems to stem from the repeated suppression of sexuality in a single species. Because the genotypes of each bisexual ancestor would inevitably be different, so too is each derived asexual lineage.

Another route depends on the ability of females that normally reproduce by parthenogenesis to retain the ability to mate with males. Because eggs produced by parthenogenetic females are diploid (as are the fertilized eggs of bisexual animals), should a potentially parthenogenetic female mate with a male, its diploid (2n) eggs and the haploid (n) sperm of the male, will give rise to a triploid (3n) individual. Triploid parthenogenetic clones of *H. incongruens* have indeed been found in Canada, and are genetically similar to what would be expected of such a mating (Turgeon & Hebert, 1994). The finding of a polyploid clone was itself interesting as it had long been thought that all parthenogenetic ostracods were diploid, though triploid forms of *Eucypris virens* had in fact been found in France. Since the discovery of polyploid clones of *H. incongruens*, study of other species has revealed further cases. Tetraploid (4n) clones of *H. incongruens* have also been found and may be the result of matings between triploid females and males with haploid sperm. However, as they could perhaps arise via an abnormal event in the development of eggs in a diploid lineage, their origin remains *sub judice*. Although the ricefield population in Italy that has at least 35 multi-locus genotypes is in an area in which males have never been found, it is possible that this clonal richness reflects recombination events in the past. Whether any of these clones are triploid is unknown.

Most remarkable of all is the origin of variability discovered by Turgeon and Hebert (1994). Near Churchill, Manitoba, parthenogenetic populations of *H. incongruens* co-exist with bisexual populations of *H. glaucus*. Among the clones of *H. incongruens* were two that were not only triploid but at four loci combined alleles otherwise unique to *H. glaucus* with others typical of *H. incongruens*. This could be the result only of matings of 'parthenogenetic' females of *H. incongruens* with males of *H. glaucus*: indeed, such copulations were observed on several occasions. It is, however, doubtful whether such hybridization is of much importance in this instance. Such hybrid polyploid clones must rarely be successful. If they were common, the genetic variability of *H. glaucus* found in that area would generate a much greater variety of clones than in fact exists. Nevertheless the phenomenon is of great interest in revealing a remarkable way in which the variability of essentially parthenogenetic clones of *H. incongruens* (and perhaps other ostracods) can be increased, and may be important in some cases.

Dispersal and related problems

How small freshwater crustaceans are dispersed has long attracted attention, but has produced little concrete information. Dispersal of *H. incongruens* is mainly by dry resting eggs. Other devices are almost certainly unimportant as active stages quickly die if removed from water and dispersal of wet diapausing eggs is probably a rare event, except perhaps in peculiar circumstances such as the flushing of a rice field. Other ostracods have been seen attached to the setae of aquatic bugs – I have myself recorded *Cyclocypris laevis* so attached (Fryer, 1953) but there appear to be no reports of *H. incongruens* doing so, and, at best, this could lead only to dispersal over short distances. *Cyclocypris ovum* has been found clinging to the skin of toads and newts (Seidel, 1989), but again an inability to survive for long out of water suggests that *H. incongruens* is seldom, if ever, so dispersed. Longer survival may be possible if the curious case of living *Cypridopsis vidua* found by Lowndes (1930) in the rectum of a frog is not an unusual event involving an ostracod, as it seems to be.

Although *H. incongruens* produces resting eggs, their dissemination appears to face formidable problems. Most are firmly attached to substrata, which must frustrate rather than facilitate dispersal. A small proportion of eggs, however, lies among bottom detritus, and others are attached to dead leaves or other objects that lend themselves to dispersal by wind – but only if they become dry and possibly disintegrate. Not all habitats dry out

regularly, and winter ice in northern latitudes must also frustrate dispersal. From sites such as horse-troughs, dispersal may be almost as difficult as colonisation. Nevertheless, wind is almost certainly the main agent of dispersal. Dried eggs are small and very light. Some may be carried to high altitudes, where similar sized particles have been found, and where conditions can be tolerated (p. 124). Any that do so may be dispersed over large distances by the strong winds that blow there. Most eggs, however, are probably less widely scattered. Even if only a small proportion of the eggs deposited each year is so dispersed, vast numbers must be scattered. For example, if in an area of 1 km^2 there is just one small pond that in the course of a season produces 10^6 adults of *H. incongruens*, and if only one dry resting egg per individual is dispersed, this is equivalent to one egg per m^2 for that area. If only 10%, or 1%, of this number of eggs is scattered, this provides one egg per 10 m^2, or 100 m^2, respectively. Such calculations are, however, unrealistic. By ignoring the properties of resting eggs, which cannot be quantified, they greatly underestimate their potential as agents of dispersal. Dry resting eggs can survive for several years. During this time they may 'alight' many times and 'sample' many prospective sites.

On the other hand, the hazards are enormous. Many eggs must be lost by lodging in terrestrial situations and some may hatch, and perish, if wetted by heavy rain, or if they alight in small temporary puddles. On this matter, a possible major destroyer of resting eggs, we have no information. Any eggs reaching the sea are also doomed. More may perish here than on land. Even inoculation of large bodies of freshwater, which is more likely than is that of small sites, and must often happen, may not be very helpful. *H. incongruens* does not flourish there. In the survey of Yorkshire, for example, it was never found in water bodies even as large as about 5,000 m^2, and many sites were very small. It is a reasonable deduction that individuals that hatch in large water bodies, and any offspring to which they give rise, are quickly eliminated. As a species so tolerant of a wide range of conditions can presumably cope with the physical environments of lakes and large ponds and find suitable food there, competition seems to be indicated. *H. incongruens* indeed bears all the hallmarks of a fugitive species – which has good colonising abilities but is easily outcompeted. Its colonising abilities are not in doubt – I have, for example found it in a small pond dug about 15 months earlier (Fryer, 1985) – and its ability to reach such remote places as Easter Island reveals its potential in this respect. Interspecific competition in horse troughs and similar situations must be minimal! Keeping it in company with other animals may throw light on its competitive abilities or deficiencies.

Comparisons with animals such as parasitic copepods of fishes are illuminating. How these find mobile hosts, which may be rare species widely separated in three dimensional space, pose what may seem to be even greater problems. However, amazing as is the location of hosts by such parasites, they have advantages over *Heterocypris*. Their dispersal stages can swim, and have sensory equipment that may guide them to a host, either directly, or in response to signals from already settled parasites, just as settling larvae of such sedentary adult crustaceans as barnacles are chemically attracted to previously settled sites. Even rare hosts may have habits that assist their parasites. They may assemble to feed, or mate, or spend periods in sleep, and some parasites conceivably disperse only for short distances. *H. incongruens* enjoys none of these advantages. It relies on chance dispersal of only a small proportion of its propagules, which lack any means of guidance to prospective sites. Comparisons with plant seeds are perhaps apposite though some seeds are scattered only in the immediate vicinity of the parent plant, and those that disperse more widely, usually by wind, have devices to enhance wind-borne transport, or to facilitate attachment to animal carriers. Target areas are also usually vastly larger than are those of *H. incongruens* whose resting eggs have no specialisations for dispersal save small size and light weight which, in the case of single eggs, are in fact probably very efficient aids. Wind-blown pollen finds much smaller targets, though there are usually many more of them, often in close proximity, and pollen grains vastly outnumber eggs of *Heterocypris*. Likewise, the number of eggs available for dispersal is minuscule in comparison with such passively dispersed propagules as fungal spores.

Dispersal in *H. incongruens* can in fact serve as a model of a widespread phenomenon. How small crustaceans locate small, isolated, but favourable habitats is still mysterious, though perhaps less so than supposed. The nearest relative of *H. incongruens* in Britain, *H. salina*, frequents brackish waters, where dispersal is probably easy, but also colonises inland saline sites, sometimes of small size. In Yorkshire, three small, widely separated sites with water of high ionic content, but different chemical composition, have been colonised (Fryer, 1993), and similar instances are known elsewhere. Formidable as are the obstacles, such animals do find rare habitats, such as inland waters of high ionic content located by *H. salina*, or small sites, such as horse-troughs, favoured by *H. incongruens*. Long-lived resting eggs, each with the potential to sample several sites, provide much of the explanation.

An important feature of dispersal in *H. incongruens* is that every individual of parthenogenetic origin that arrives in a suitable habitat is a potential founder of a new population. Were it necessary for a male and a female to colonise such sites as horse-troughs, the chances of establishing populations there would be extremely low. As only one coloniser is required, the chance of success is greatly increased. Herein lies a great advantage of parthenogenesis, and one that appears to have received inadequate recognition in theoretical discussions.

H. incongruens as a possible ancient asexual

A general inference about asexual animals is that they generally persist for only short periods of time. Genetic studies confirm that many of them are of recent origin and that persistent lineages rely on the infusion of genetic variation from sexual relatives. Nevertheless a few asexual lineages are believed to be ancient. It is difficult to decide whether the genetic diversity of these is the result of mutation since they became asexual or of intermittent input from sexual relatives. Using both mitochondrial DNA (which is inherited entirely maternally) and allozyme data (technical details of which are unnecessary here) attempts have been made to estimate the age of unisexual lineages of *H. incongruens* (Chaplin & Hebert, 1997). An incidental, and completely unexpected, result was that at the one site at which the two co-existed, *H. incongruens* displayed considerably more diversity than the sexual *H. glaucus*!

Divergence between clones was found to be substantial in both the nuclear and mitochondrial genomes. A strong correlation in the extent of nuclear and mitochondrial divergence between pairs of clones suggests that *H. incongruens* is an ancient asexual which has undergone considerable mutational divergence. Indeed by calculating the rate of sequence divergence in mtDNA (and adopting a conservative value for a somewhat contraversial procedure) it was estimated that it has persisted as an asexual for more than 5 million years. Acceptance of such a figure is provisional but there is a distinct possibility that asexuality is indeed an ancient attribute of some lineages of *H. incongruens*. If so, this remarkable ostracod has another claim to distinction.

An historical irony

H. incongruens has another modest, and unexpected, claim to fame. In view of the great rarity of males it is ironical that it was in this species that sperms of ostracods were first recorded. Ramdohr (1808), the describer of *H. incongruens*, saw them when making a dissection but, although they came from the sperm duct, didn't recognise them as sperms. This is not surprising for they are of enormous length. Wingstrand (1988), who had access to males from Palestine, gives their length as 1.3 mm, that is about the same length as the animal itself. Ramdohr saw them straighten out into hair-like structures after their release and wondered if they were 'Blutgefüsse' (blood vessels)! Not until almost 30 years later did Wagner recognise them for what they were. Giant sperms of ostracods (some are considerably longer than those of *H. incongruens*) have received much study but it is a curious and little-known fact that they were first seen in a species in which most populations consist entirely of females! It is surprising that Sars (1928), who notes that he

never saw a male of *H. incongruens*, and who cites Ramdohr's paper, does not mention the latter's observation.

Some unsolved conundrums

What seems on first acquaintance to be the simple life cycle of *H. incongruens* turns out in fact to be very complex. Although much has been learned, unsolved problems remain. It is, for example, curious that what have been taken to be genetically identical individuals, kept under the same conditions, may differ considerably in such things as life span and fecundity. A possible explanation is that in fact they belong to different, unrecognised, clones, or less likely, the differences are due to infections of which the observer is unaware, or even to mutations. More problematic is why genetically identical eggs produced by a single female, laid at the same time or within a few days of each other, and kept under the same conditions, may either hatch within a few days or remain dormant for long periods. How these different programmes for development operate and, even more remarkable, how a single parthenogenetic female can lay a mixture of such eggs, remain unknown.

The existence of genetically different clones has been firmly established, and clear ecological differences (particulary seasonal requirements) have been demonstrated between clones, but there are still problems as to how, if at all, clones are cued to produce the kinds of eggs appropriate for their particular life cycles, or whether they rely on the production of their mysterious mixtures of eggs whose products are simply sorted by climatic conditions. The same is true of stimuli that induce hatching of diapausing eggs whose nature remains obscure and difficult to investigate. While there is evidence that eggs of different seasonal clones differ in this respect, the differences are not really understood, nor is their significance in nature. There is also the question of what determines whether dry resting eggs hatch when they first become wet, or require more than one such wetting. The value of variability in this respect is self-evident, but how it is achieved remains obscure.

The genetic nature of populations in horse-troughs remains to be investigated. While one is tempted to predict that there will usually be only one clone per trough, this remarkable ostracod has produced so many surprises that it would be rash to make this assumption. It would also be interesting to know whether adjacent troughs share the same clone(s). A place like Sark with at least three trough populations in close proximity, yet well isolated from adjacent populations, may provide clues about patterns of dispersal.

Another problem is how *H. incongruens* maintains genetic variability. Rapid loss of genetic variation in parthenogenetically reproducing *Daphnia* has been demonstrated see p. 126). Many populations of *Daphnia* can restore this variability by periodic bouts of sexual reproduction. This is not an option in unisexual populations of *H. incongruens*, e.g. in Britain, yet these populations persist and are clearly successful. Some populations of *D. pulex* consist of obligate parthenogens. As a group these harbour as much variation in quantitative traits as do those that reproduce sexually. This seems to be due to the high rate of origin of obligate parthenogenesis. This cannot be the case in *H. incongruens* in areas where there are no bisexual populations from which parthenogenetic forms could be repeatedly derived, and certainly not if some lineages are ancient asexuals. Nevertheless, in some areas in which males are unknown, as in certain Italian ricefields, a rich diversity of electrophoretic clones may be present. How do these manage to survive so much better than, apparently, do obligately parthenogenetic *Daphnia*?

The roles of environment and heredity in the determination of the size of individuals in different seasonal clones remain to be clarified. Early observations on such clones overlooked environmental influences but nevertheless suggest that genetic differences between clones may be involved.

More information is needed on the structure of the eggs, on how they are attached to objects, whether there are physical differences between slow- and fast-developing eggs (which at present can only be recognised on the basis of their performance), on the nature of the yolk granules, on embryology, on what happens to eggs when they become dry and

when they are rehydrated. What gives dry eggs their amazing resistance is a problem common to a wide range of resting eggs, and is not really understood.

Finally, one wonders what it is about horse-troughs and similar receptacles that makes them so attractive to this common ostracod.

Concluding remarks

The life cycle and ecology of *H. incongruens* present many problems. When to these are added others posed by the variation in the eggs, the amazing resistance of resting eggs, and their dispersal, it becomes apparent that we really know very little about some important aspects of the life of this interesting animal. The horse-trough ostracod is truly worthy of attention.

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References

Angell, R. W. and Hancock, J. W. (1989). Response of eggs of *Heterocypris incongruens* (Ostracoda) to experimental stress. *J. Crust. Biol.* **9**: 381-386.

Benzie, J. A. H. (1984). Small scale diurnal migrations by *Heterocypris incongruens* (Ramdohr, 1808) Ostracoda: Cyprididae) in a temporary pool, Ghana, West Africa. *J. Crust. Biol.* **4**: 63-65.

Bronshtein, Z. S. (1947). Freshwater Ostracoda. *Fauna of the USSR Crustaceans* Vol. 2, No. 1 (In Russian, Eng. Transl. 1988).

Cáceres, C. E. (1997). Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. (In prep.)

Carlisle, D. B. (1968). *Triops* (Entomostraca) eggs killed only by boiling. Science. **161**: 279.

Carvalho, G. R. (1987). The clonal ecology of *Daphnia magna* (Crustacea: Cladocera) II Thermal differentiation among thermal clones. *J. Anim. Ecol.* **56**: 469-478.

Carvalho, G. R. (1988). Differences in frequency and fecundity of PGI-marked genotypes in a natural population of *Daphnia magna* Straus (Crustacea: Cladocera) *Funct. Ecol.* **2**: 453- 462.

Carvalho, G. R. and Hughes, R. N. (1983.) The effect of food availability, female culture-density and photoperiod on ephippia production in *Daphnia magna* Straus (Crustacea: Cladocera) *Freshwat. Biol.* **13**: 37-46.

Chaplin, J. A. and Hebert, P. D. N. (1997). *Cyprinotus incongruens* (Ostracoda): an ancient asexual? *Molec. Ecol.* **6**:155-168.

Coker, R. E. (1933). Influence of temperature on size of freshwater copepods (Cyclops). *Int. Rev. Hydrobiol. Hydrogr.* **29**: 406-436.

Dumont, H. J. and Martens, K. (1996). The freshwater microcrustacea of Easter Island. *Hydrobiologia* **325**: 83-99.

Fox, H. M. and Taylor, A. E. R. (1955). The tolerance of oxygen by aquatic invertebrates. *Proc. R. Soc. Lond B.* **143**: 214-225.

Fryer, G. (1953). Notes on certain British freshwater crustaceans. *Naturalist* **78** :101-109.

Fryer, G. (1985). Crustacean diversity in relation to the size of water bodies: some facts and problems. *Freshwat. Biol.* **15**: 347-361.

Fryer, G. (1993). *The freshwater Crustacea of Yorkshire: a faunistic and ecological survey.* Yorks. Nat. Union & Leeds Phil. Lit. Soc.

Ganning, B. (1971). On the ecology of *Heterocypris salinus, H. incongruens* and *Cypridopsis aculeata* (Crustacea: Ostracoda) from Baltic brackish-water rockpools. *Mar. Biol.* **8**: 271-279.

Green, J. (1959). Pigmentation of an ostracod, *Heterocypris incongruens*. *J. Exp. Biol.* **36**: 575-582.

Griffiths, H. I. and Butlin, R. K. (1995). A timescale for sex versus parthenogenesis: evidence from subfossil ostracods. *Proc. R. Soc. B.* **260**: 65-71.

Hairston, N. G. Jr., van Brunt, R. A., Kearns, C. M. and Engstrom, D. R. (1995). Age and

survivorship of diapausing eggs in a sediment egg bank. *Ecology* **76**: 1706-1711.
Havel, J. E., Hebert, P. D. M. and Delorme, D. (1990). Genotypic diversity of asexual Ostracoda from a low arctic site. *J. Evol. Biol.* **3**: 391-410.
Klie, W. (1938). Krebstiere oder Crustacea. III Ostracoda, Muschelkrebse. *Die Tierwelt Deutschlands*. **34**: 230 pp.
Lowndes, A. G. (1930). Living ostracods in the rectum of a frog. *Nature Lond* **76**: 958.
Lynch, M. (1984). The limits to life-history evolution in *Daphnia*. *Evolution* **38**: 465-482.
Ramdohr, F. A. (1808). Über die Gattung *Cypris* Müll. und drei zu derselben gehörige neue Arten. *Magazin Ges. naturf Freunde Berlin* **2**: 83-93.
Rossetti, G. and Martens, K. (1996). Redescription and morphological variability of *Darwinula stevensoni* (Brady and Robertson, 1870) (Crustacea, Ostracoda). *Bull. Inst. R Sci. Nat. Belg. Biol.* **66**: 73-92.
Rossi, V. and Menozzi, P. (1990). The clonal ecology of *Heterocypris incongruens* (Ostracoda). *Oikos* **57**: 388-398.
Rossi, V. and Menozzi, P. (1993). The clonal ecology of *Heterocypris incongruens* (Ostracoda): life history traits and photoperiod. *Funct. Ecol.* **7**: 177-182.
Rossi, V., Gandolfi, A. and Menozzi, P. (1996). Egg diapause and clonal structure in parthenogenetic populations of *Heterocypris incongruens* (Ostracoda). *Hydrobiologia* **320**: 45-54.
Rossi, V., Giordano, P. and Menozzi, P. (1993). Genetic variability in parthenogenetic populations of *Heterocypris incongruens* (Crustacea, Ostracoda). In *Ostracoda in the earth and life sciences* (ed. McKenzie, K. G. and Jones, P. J.), *11th Int. Symp. Ostracoda* 369-383.
Rossi, V., Rossi, M. C. and Menozzi, P. (1991). Life strategy differences among electrophoretic clones of *Heterocypris incongruens* (Crustacea, Ostracoda) *Verh. Internat. Verein. Limnol.* **24**: 2816-2819.
Sars, G. O. (1928). *An account of the Crustacea of Norway. Vol. 9 Ostracoda*. Bergen Museum.
Seidel, B. (1989). Phoresis of *Cyclocypris ovum* (Jurine) (Ostracoda, Podocopida, Cyprididae) on *Bombina variegata variegata* (L) (Anura, Amphibia) and *Triturus vulgaris* (L) (Urodela, Amphibia). *Crustaceana* **57**: 171-176.
Sohn, I. G. and Kornicker, L .S. (1979). Viability of freeze-dried eggs of the freshwater *Heterocypris incongruens*. In N. Kristic, ed. *VII Int. Symp. Ostracoda* 1-3.
Spitze, K. (1991). *Chaoborus* predation and life history evolution in *Daphnia pulex*: temporal pattern of population diversity, fitness and mean life-history. *Evolution* **45**: 82-92.
Sywula, T. E. and Lorenc, R. (1982). Esterase polymorphism as a marker of interpopulation differentiation in *Cyprinotus incongruens* (Ramd). (Ostracoda, Crustacea) *Bull. Acad. Poln. Sci.* **29**: 317-322.
Turgeon, J. and Hebert, P. D. N. (1994) Evolutionary interactions between sexual and all-female taxa of *Cyprinotus* (Ostracoda:Cyprididae). *Evolution* **48**: 1855-1865.
Wingstrand, K. G. (1988). Comparative spermatology of the Crustacea Entomostraca 2. Subclass Ostracoda. *Biol. Skrift. Kongel. Danske, Vidensk. Selskab.* **32**: 1-118.

BOOK REVIEWS

Wildlife Conservation in Managed Woodlands and Forests by **Eamond Harris** and **Jeanette Harris**. Pp. xiv + 342, illustrated. Research Studies Press, Taunton/John Wiley, New York. 2nd edition. 1997. £25.00 paperback.

Based on their observations and experience, as well as a detailed survey of the literature, the authors provide an account of how present-day managed forests have become what they are and discuss ways of improving their conservation potential. Particular attention is paid

to British woodlands, a major section dealing with the different groups of fauna and fauna in productive woodlands and forest and the conservation measures necessary for protecting them.

Nature Reserves – who needs them? Edited by **T. G. Lawson** and **T. M. Reed.** Pp. 106. Joint Nature Conservation Committee. 1997. £25.00 plus postage & packing from JNCC, Monkstone House, City Road, Peterborough PE1 1JY.

Proceedings of a conference held by the Nature Conservancy Council in Birmingham in 1991: an opening address by Sir John Burnett is followed by 16 papers which comprehensively cover the subject (e.g. acquisition, management, function, amenity, finance, monitoring, research, education), a workshop feedback to the plenary session, and a concluding synthesis.

The Earth Under Threat: a Christian Perspective by **Ghillean Prance**. Pp. 92. with b/w plates. Wild Goose Publications, Glasgow. 1996. £6.99 paperback.

Sir Ghillean Prance, Director of the Royal Botanic Gardens, Kew, examines many environmental issues which confront us today from a Christian perspective. His book, based on the 1995 Templeton Lectures, explores our role as caretakers and stewards of the earth in a style that brings alive the author's scientific insights in a most readable manner.

Hitherto by **Albert G. Long**. Pp. xvi + 278, illustrated. The Pentland Press, Edinburgh. 1996. £15.50 hardback.

Autobiographical account by the palaeobotanist Dr Albert Long, former Deputy Director at the Hancock Museum, Newcastle, born and educated in Lancashire. Long's strong Christian beliefs are evident in his memoir, which covers a lifetime of natural history study and teaching, with an emphasis on his special interest in the fossil flora of N.E. England and S.E. Scotland.

Seaweed Ecology and Physiology by **Christopher S. Lobban** and **Paul J. Harrison**. Pp. ix + 366, illustrated. Cambridge University Press. 1997. £19.95 paperback.

A major rewrite of an earlier work, *The Physiological Ecology of Seaweeds* (1985), which now provides not only an extensive survey of the literature but also guest essays by noted ecologists. More attention is paid in the revised version to tropical seaweeds and habitats, as well as the better-known temperate ecosystems. Well written and presented, and encyclopaedic in its scope.

Alien Grasses of the British Isles by **T. B. Ryves, E. J. Clement** and **M. C. Foster** (with guidance on nomenclature by **D. H. Kent**, illustrations by **G. M. S. Easy**, and an index by **R. Gwynn Ellis**). Pp. xxi + 181. Botanical Society of the British Isles. 1996. £10.50 paperback, from BSBI Publications, Green Acre, Wood Lane, Oundle, Peterborough PE8 5TP.

Companion volume to Clement and Foster's *Alien Plants of the British Isles* published by the BSBI in 1994 (see *Naturalist* **121**: 36, 1996) providing a detailed list of grasses introduced into this country over the past 200 years which includes data on habitat, frequency, status, origin and means of introduction. The list is followed by keys to the Bambuseae (by D. T. Holyoak) and some larger and more difficult genera, the whole ably supported by 29 pages of line drawings and a detailed index with full synonymy.

DIET OF BARN OWLS *TYTO ALBA* IN A LOWLAND AREA OF NORTH YORKSHIRE

J. ROBERTS, G. W. SCOTT[1] AND S. L. HULL
School of Science and Management, University College Scarborough, Filey Road, Scarborough, YO11 3AZ

ABSTRACT

Samples of Barn Owl *Tyto alba* pellets were collected from a lowland area of North Yorkshire during the spring and summer of 1995. Microscopic analysis of their contents provides information about the diet of the study population and highlights the nutritional importance of small mammals which account for 95% of all prey taken. The field vole *Microtus agrestis* was recorded as being the most important single species in the diet, accounting for half of all prey consumed.

INTRODUCTION

Analysis of the contents of regurgitated owl pellets offers a convenient insight into both the diet of the species of owl concerned and also into the constitution of the community upon which they prey. The Barn Owl is, in Britain, at the northern limit of its range and has in recent times become a subject of conservation concern. The species is now restricted to just a few strongholds in the British Isles (Gibbons *et al.*, 1993), with many populations dependent to some degree upon the provision of artificial nest sites. In this study we investigate the diet of such a population inhabiting the mixed agricultural land of the Vale of Pickering, North Yorkshire.

METHODS

Study site and pellet collection

345 pellets were collected from barn owl nest sites during regular ringing and monitoring work (carried out under license), and from sites within their hunting ranges. The areas concerned are all within the Vale of Pickering and at approximately 20 m above sea level. The study area is a mosaic of mixed agricultural land with few large human settlements and little woodland. It is crossed by a number of water courses ranging in size/volume from rivers such as the Derwent, to streams and drainage ditches. The majority of the area's field boundaries support little more than a 2 m belt of unmanaged grassland.

Collection of pellets was carried out twice. A spring collection was made in April 1995 and it is assumed that these pellets contained prey consumed during late winter and early spring. The second sample was collected (where possible from the same sites) during the summer months (June and July 1995) and is assumed to have contained prey consumed during late spring and early summer.

Pellet analysis

The length of all pellets was recorded. Small fragments of pellet from a single site were 'reconstructed' to produce a pellet of average length. Pellet width was not found to vary greatly and was not systematically recorded (though we estimate that all pellets were 25-28 mm in diameter). After measuring, the dry pellets were gently teased apart and their contents retrieved for identification. Obvious material was removed (skulls, long bones etc.) and the matrix of the pellet was then examined under a stereo-microscope in order that smaller remains (insect parts etc.) might be collected.

Identification of prey items

Skull and jaw remains were used to identify mammalian and avian prey and their numbers

[1]Author for correspondence (email: grahams@ucscarb.ac.uk

were established by a skull count (Corbett & Harris, 1993; Glue, 1974; Julian & Altringham, 1994). As Barn Owls are known to decapitate avian prey regularly prior to ingestion (Glue, 1967), feather material, a sacrum, a sternum or long bones were used as indicators of avian presence. It was not possible to separate the remains of Wood Mice *Apodemus sylvaticus* and Yellow-necked Mice *Apodemus flavicollis* and for the purposes of this study the two are grouped as wood mouse.

The lower jaws and pelves of shrews *Sorex* spp. were retained during sorting and used to age and sex individuals so that an assessment of shrew prey population structure might be made. Shrews were aged according to tooth wear and sexed according to pelvis shape after Yalden and Morris (1990). When establishing the frequency of individuals in each age/sex class, jaws/pelves were paired, with each additional jaw/pelvis counting as one individual.

Invertebrates were identified from chaetae (earthworms), or heads and elytra (beetles) and their numbers were approximated.

Estimates of the mass of mammalian prey items consumed (relative mass being an indicator of the relative nutritional value of prey types) were obtained from the available literature (Julian & Altringham, 1994; Yalden & Morris, 1990). The mass of invertebrate prey items was estimated by the authors. If avian remains could not be identified to a species, an average mass of 15g was recorded after Julian and Altringham (1994).

Results

A total of 345 pellets was collected, from which 1,616 prey items were retrieved. Pellets ranged from 20 mm to 90 mm in length (mean ± standard deviation = 49.5 ± 11.2).

Sample 1 (hereafter spring) produced a total of 589 prey items from 122 pellets. The highest number of items recovered from a single spring pellet was 10 – a combination of only Common Shrew *Sorex araneus* and Pygmy Shrew *Sorex minutus*. The mean weight of spring prey items was estimated as 13g. Sample 2 (hereafter summer) consisted of 223 pellets containing 1,027 prey items. The highest number of items recovered from a single summer pellet was 13, again a mixture of Common Shrew and Pygmy Shrew with a single Field Vole; this was also the largest pellet analysed (90 mm x 28 mm). The mean weight of summer prey items was estimated as 15g. Two of the summer sample pellets comprised solely vegetable material (grass and straw). It was initially assumed that such material might indicate the presence of invertebrate remains but none was found. Similar pellets have been reported by Shawyer (1994) but an explanation of their existence remains elusive.

Table 1 summarises the data collected (spring and summer combined). A total of 10 species of mammals was recorded in the diet of the Barn Owl population. Of these, Field Vole and Common Shrew were the most commonly recorded prey items and together accounted for more than 70% of the total prey intake (in term of numbers of animals caught). In terms of their relative nutritional importance (proportion of the total prey weight) Field Voles appear to be disproportionately important, accounting for 51.8% of prey weight (in comparison with their numerical importance) with Common Shrew, Wood Mouse and Bank Vole *Clethrionomys glareolus* making up the bulk of the remainder of the diet. All other species appear relatively unimportant (although of course they clearly are important if considered as a single unit).

Figures 1a and 1b illustrate the seasonal importance of the various prey types. Figure 1a reveals that Common Shrew accounted for 24.7%, Wood Mouse for 9% and Field Vole for 51% of the total prey items recorded in spring. Whilst the Field Vole still accounted for 51% of the diet in summer (Figure 1b), Common Shrew decreased in importance (30% to 16.9%) and the Wood Mouse increased in importance from 9% in spring to 18.4% in summer. The summer diet is more varied than the spring diet (χ^2 test to compare the relative frequencies of prey types in the two samples; $\chi^2 = 53.73$, d.f = 12, $p<0.001$) (Sokal and Rholf, 1991). In both samples the single most important species is the Field Vole (*c.* 52% by weight). Of the other important species, Bank Vole appears relatively constant in value (8-10% by weight).

TABLE 1

Summary of barn owl diet from pellet analysis (pooling spring and summer samples). Prey weight (%) is the prey by weight, expressed as a % of the weight of all prey. All values for prey weights are from Yalden and Morris (1990). Beetle weight was estimated by the authors. Bird weights were calculated assuming a mean weight of 15g (Altringham *et al.*, 1994).

		N. prey	% of total prey	mean item weight (g)	total prey weight (g)	prey weight as a % of diet
MICTROTINES						
Field Vole	*Microtus agrestis*	571	35.3	21	11991	51.8
Bank Vole	*Clethrionomys glareolus*	123	7.6	16	1968	8.5
Water Vole	*Arvicola terrestris*	1	0.2	100	100	0.4
MURIDS						
Wood Mouse	*Apodemus sylvaticus*	193	11.9	14	3474	15
House Mouse	*Mus musculus*	13	0.8	12	156	0.7
Harvest Mouse	*Micromys minutus*	5	0.3	5	25	0.2
Brown Rat	*Rattus norvegicus*	3	0.2	60	180	0.8
SHREWS						
Common Shrew	*Sorex araneus*	563	34.8	8	4504	19.4
Pygmy Shrew	*Sorex minutus*	112	6.9	4	448	1.9
Water Shrew	*Neomys fodiens*	17	1.1	12	204	0.9
BIRDS	**Total**	5	0.3		80	0.3
Chaffinch x 2	*Fringilla coelebs*			44		
Parus species x 2	*P. caeruleus* or *ater*			21		
Unidentified x 1				15		
BEETLES		4	0.2	1	4	0.01
Scarabaeidae						
Summer Chafer	*Amphimallon solstitialis*					
Silphidae						
	Necrodes littoralis					
	Necrophorus humator x 2					
ANNELIDA						
Earthworms	*Lumbricus* species	6	0.4	5	30	0.1
TOTAL		1616	100		23168	100

The population structure of the shrews recovered from the spring (205 individuals, 30% of the total spring prey) and summer (210 individuals, 30% of the summer total prey) pellet samples indicates that spring pellets contain a higher proportion of older animals, whilst younger animals account for a higher proportion of the prey in the summer pellets (χ^2 = 30.67, d.f = 3, $p<0.001$). Both samples contained a predominance of male animals (χ^2 = 11.95, d.f = 1, $p<0.001$) although in summer the sex bias was not quite so pronounced, with males accounting for 65% of the summer sample and 80% of the spring sample.

Discussion

A puncture wound at the back of most of the recovered mammal and bird skulls was assumed to have been the killing method employed most frequently by the owls of this

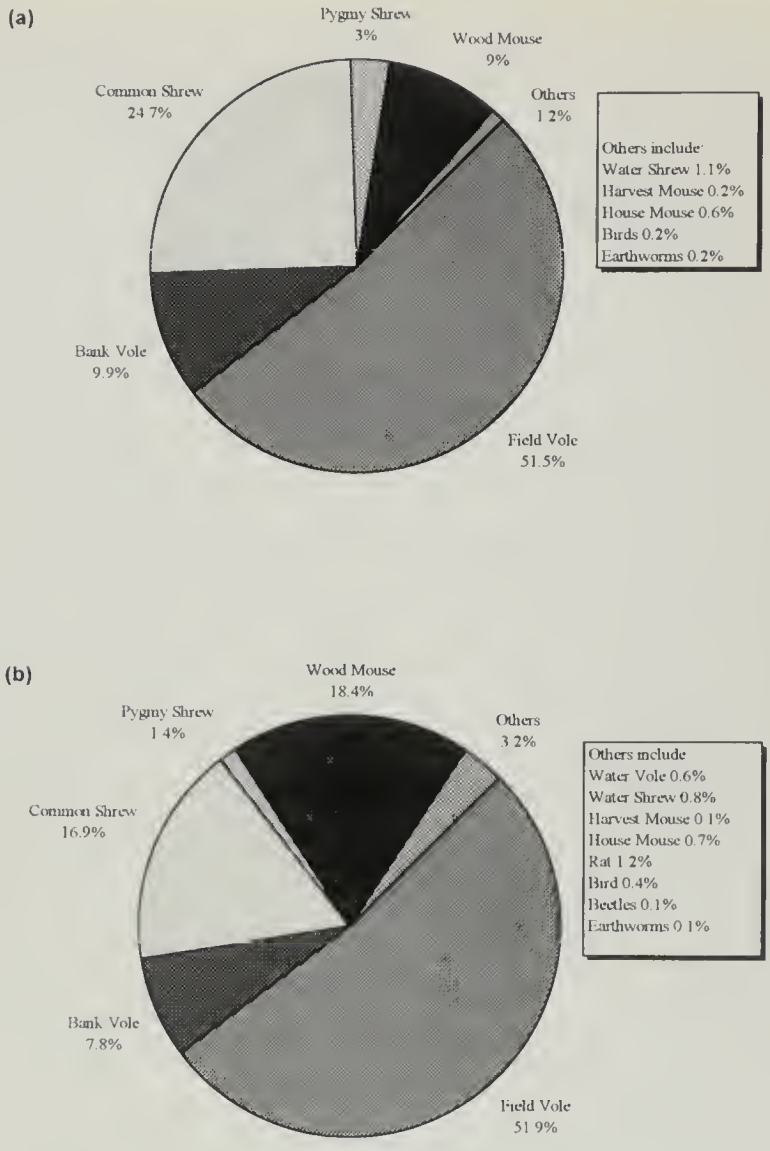

FIGURE 1
Prey items identified in (a) spring pellet sample analysis and (b) summer pellet sample analysis. Prey items represent a % by weight of total prey weight.

study population, although Raczyinski and Rupreeht (1974) have recorded that damage to skulls is usually less common in the prey of Barn Owls when compared to species such as the Tawny Owl *Strix aluco* or Little Owl *Athene noctua*. Such damage, which facilitates skull digestion, made it necessary to identify some remains from jaws and long bones. It was also noted that a number of pellets contained under-digested material, a situation which probably reflects high prey abundance where the stimulation of the next meal triggers premature regurgitation (Lowe, 1980).

As with the majority of previous studies of Barn Owl diet, the Field Vole was identified as being the main prey species of this population in both seasons. Although more shrews than voles were caught in spring, the Field Vole consistently provided the highest nutritional value (as a percentage of the total prey weight). The relative proportions of voles and shrews in Barn Owl diets have been discussed by Webster (1973) (who suggested that a fall in dietary vole numbers results in a disproportionately large numerical

increase in shrew prey, ensuring that the owls achieve their nutritional requirement), and by Bunn *et al.* (1982), who suggest that a vole/shrew ratio relationship is typical of British pellet analysis. We observed a relatively constant (by weight) vole component to the diet of our study population but did note a shift in the relative value of shrews and Wood Mice, presumably a response by the birds to the need to balance primary and secondary prey consumption in order to maintain nutritional intake.

In addition to the shift in the relative importance of shrews in the diet of the owls, examination of the population structure of the shrews captured shows that in spring, when shrew numbers were higher, more males than females were recorded and the majority of the animals were older individuals. In summer more males were recorded but the bias was lower and the percentage of younger animals was higher. Similarly Brown (1981) has reported that 61% of the shrews recovered from Barn Owl pellets in May are male. Corbett and Harris (1993) have suggested that males are more likely to be caught than females because they spend more time above ground vigorously defending their territories and are thus exposed to a higher predation risk; this is particularly the case in spring. The younger animals in the summer sample are presumably put at predation risk during post-weaning dispersal involving both sexes (May onwards; Butterfield *et al.*, 1980), hence the relative increase in the number of females recorded.

In some parts of the Barn Owls' range (and especially on arable land) the Brown Rat *Rattus norvegicus* is a major component of the diet (Glue, 1974). As rats can weigh more than 500g (Corbett & Harris, 1993), it is likely that attacks would concentrate upon younger animals. In this study the rat did not represent a major prey component, and the animals which were recorded were relatively small. Similarly, House Mouse *Mus musculus* and Harvest Mouse *Micromys minutus*, whilst important in some studies of the diets of owls were of little importance in this study, probably as a result of the relatively small amounts of suitable habitat for these species in the study area.

In common with previous work (Glue, 1974), birds formed a relatively unimportant proportion of the diet of the owls. The species caught were common woodland/hedgerow birds, Coal Tit *Parus ater*, Blue Tit *P. caeruleus* and Chaffinch *Fringilla coelebs*, and the slight increase in their importance in summer may be due to the increased availability of fledglings. Similarly, invertebrates did not form a major component of the diet. Earthworms were recorded from three pellets and beetles were recorded only from the summer sample. Shawyer (1994) has suggested that invertebrates, particularly beetles (Mikkola, 1983), may be consumed by adult birds during the raising of young when most mammalian prey must be given over to their chicks.

Acknowledgments

We would like to express our gratitude to Pawl Willet and David Jardine who provided the pellets used in this study.

References

Brown, D. J. (1981). Seasonal variations in the prey of some Barn Owls in Gwynedd. *Bird Study* **28**: 139-146.

Bunn, D. S., Warburton, A. B. and Wilson, R. D. S. (1982). *The Barn Owl* T. & A. D. Poyser, Carlton.

Butterfield, J., Coulson, J. C. and Wanless, S. (1980). Studies of the distribution of Pygmy and Common Shrews in Northern England. *J. Zool., London*. **195**: 169-180.

Corbett, G. B. and Harris, S. eds. (1993). *The Handbook of British Mammals*. 3rd edition. Blackwell, Oxford.

Gibbons, W. G., Reid, B. R. and Chapman, R. A. (1993). *The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991*. T. & A. D. Poyser, Carlton.

Glue, D. E. (1967). Prey taken by the Barn Owl in England and Wales. *Bird Study* **14**: 169-183.

Glue, D. E. (1974). Food of the Barn Owl in Britain and Ireland. *Bird Study* **21**: 200- 210.

Julian, S. and Altringham, J. D. (1994). Bat predation by a Tawny Owl. *Naturalist* **119**: 49-56.
Lowe, V. P. W. (1980). Variation in digestion of prey by the Tawny Owl (*Strix aluco*). *J. Zool., London* **192**: 283-293.
Mikkola, H. (1983). *Owls of Europe*. T. & A. D. Poyser, Carlton.
Raczyinski, J. and Ruprecht, A. L. (1974). The effect of digestion on osteological composition of owl pellets. *Acta Ornithol.* **14**: 25-38.
Shawyer, C. R. (1994). *The Barn Owl*. Hamlyn, London.
Sokal, R. R. and Rholf, F. J. (1991). *Biometry*. 2nd edition. Freeman. New York.
Webster, J. A. (1973). Seasonal variation in mammal contents of Barn Owl castings. *Bird Study* **20**: 185-196.
Yalden, D. W. and Morris, P. A. (1990). The analysis of owl pellets *Occasional Publications of the Mammal Society* No. 13. The Mammal Society, London.

BOOK REVIEWS

The Making of the Cretan Landscape by **Oliver Rackham** and **Jennifer Moody**. Pp. xvii + 237 with numerous line drawings & maps, + 4 pp. of colour plates. Manchester University Press. 1997. £50.00 hardback, £19.99 paperback.

A remarkable natural landscape with a rich archaeological heritage. Through field observations, archaeology, ancient and medieval documents, place-names, dendrochronology and standing buildings, the authors demonstrate how the island's wonderful and dramatic features have been moulded and modified by centuries of human activity.

Charles Waterton: a Biography by **Brian W. Edginton**. Pp. xi + 254, with 40 b/w plates. Lutterworth Press, Cambridge. 1996. £25.00, hardback.

The eccentric but nevertheless gifted Yorkshire naturalist Charles Waterton (1782-1865) was a, if not the, pioneer of nature conservation, converting the 250 acre estate around his home, Walton Hall near Wakefield, into probably the world's first nature reserve. However, he is best remembered for his *Wanderings in South America*, a best-selling work which has never been out of print since its first publication in 1825.

Five biographies of Waterton and innumerable papers about him have been published prior to this one. The latest undoubtedly contains new information and fresh interpretations, but unfortunately it lacks co-ordination. Information spills out in an illogical manner: the author is easily side-tracked, thus often spoiling the chronological sequence through the use of quotations apparently included in order to score points rather than for any real relevance to the author's argument. The author is also prone to journalese and slang, as exemplified by such expressions as 'little Lord Waterton', 'young massa', 'boffins', 'hubble bubble' and 'load of old bull'. The author's lack of a scientific background is all too evident: he writes of 'animals' rather than 'mammals', uses incorrect Latin nomenclature and poor terminology (e.g. rain acid) and his interpretation is inadequately researched. Spelling mistakes and inconsistencies within the text and index have also been noted.

It has long been recognised that Waterton is a very unreliable source and his recollections can be untrustworthy and contradictory. This latest biographical treatment of him has some merit in trying to set the record straight, but all-in-all the presentation lacks authority due to the haphazard manner in which the information is provided. Nevertheless, those interested in the history of natural history and naturalists in general, particularly those in Yorkshire, will find much to interest them in this biography.

MRDS

OBITUARY
GEORGE ROWLAND EDWARDS
1910-1996

George Edwards was born in Halifax on 16th February, 1910 and died in Eastleigh, Hampshire on 19th July, 1996. He was the youngest of a family of five, with a sister and three brothers. His sister remembers that he was always fascinated with wildlife and in his earliest diaries in 1925 and 1926 he mentioned animals and flowers he had seen as well as his daily bird list. These diaries he wrote up to the day he died; they provide an excellent record of his travels at home and abroad. He was one of the founder members of the Halifax Zoological Group in 1932. The moorland reservoirs, especially the Gorple group and White Holme, and the Calder valley, especially Elland sewage farm, were visited regularly by members of the Group in Spring and Autumn. These visits showed there were annual movements of waders through the area and accounts of these were published in *The Naturalist*. In 1947, a ringing station was established at High Royd sewage farm, the first inland site in Britain. Then, in 1949, just after the Group merged with the Halifax Scientific Society, there was excitement when a Desert Wheatear was found on the local moors near the appropriately named farm, 'Egypt'.

By the early 1930s he was travelling more widely in the county and in Britain. In 1934, on a trip to Scotland, he recorded 13th June as Temminck's Stint day when the first nest for Britain was found in Speyside. In the same year, he visited Spurn for the first time, followed by a further seven visits up to 1939, including one with some of the Halifax Zoological Group in 1936, an account being published in *The Naturalist*.

He soon developed an interest in photography, probably encouraged by his elder brother, and, in 1933, turned to cinephotography for birds. With Vernon Crapnell, his friend and regular companion with a similar interest, he must have been one of the first wildlife cinephotographers in Yorkshire. A year later, he was capturing Temminck's Stint on film. Nearer home, from a mill roof in Stainland, he filmed a rookery and, at High Royd sewage farm, the display of Redshanks. Before the 1939-45 war he worked for the family firm of Edwards and Sons, a furnishing business housed in a two-storey building with a tower. He used this tower as a studio for titling and editing films and a place for making photographic hides.

During the war he served in the Auxiliary Fire Service, based in Halifax and seconded to Bradford and Hull during their air raids. After the war George decided to take up a career filming wildlife. In the late 1940s and early 1950s he worked as a field assistant to Eric Hosking, making films in the summer and giving shows of his own films and those he had made for the R.S.P.B. in the winter. With Eric Hosking and Stuart Smith he also studied the aggressive display of Ringed Plovers and Oystercatchers with the use of stuffed specimens and a mirror and the reactions of some passerine species to a stuffed Cuckoo. Papers describing this work were published in *British Birds* in 1947-1950. In January 1953 he joined the staff of the R.S.P.B. to set up a film unit, making films and giving shows until he left in January, 1957. He was the ideal man for the job at that stage. In 1957 he was assistant warden on Skokholm for seven months. In 1958 it was back to filming with a five-month trip on a tanker from Holland to the Persian Gulf and back. In December 1958, he made two round-the-world trips in the southern oceans as Purser's writer, and in December 1959 and November 1960, he was filming for the Falkland Islands Dependencies' Survey (now the British Antarctic Survey). In 1963, he made three trips on British India cruise ships, two into the Mediterranean and one to Madeira and North Africa, when he showed slides and films to school parties and also demonstrated there could be things to see at sea between the ports of call! In 1964 there was a similar trip to Reykjavik and Norway.

From late 1964 until he retired in 1975, he made films for the Anglia TV 'Survival' Series. These took him to distant and remote places: to the Falklands and Antarctica again, to Tristan da Cunha, Aldabra, Natal, Trinidad and Tobago, Panama and Venezuela and

Israel, as well as various assignments in Britain including St. Kilda, Orkney and Hilbre Island. He also made a film, 'The Spider's Web' for the Yorkshire Naturalists' Trust (now the Yorkshire Wildlife Trust).

During all the time to 1971, Halifax was his home base but, whenever he returned to Yorkshire between his travels, he spent most of his time, sometimes lengthy periods, at Spurn where the Bird Observatory had been established in 1945 and which he helped a great deal in the early days. He also stayed at Eastleigh with his sister and moved his home base there in July, 1971. After his retirement he visited Spurn annually up to 1986 and again, in 1990 and 1991, his final visits.

Rowland, George's middle name, was chosen by his father as he was an admirer of Rowland Hill, the 'stamp man'. There might have also been a painting connection as George's father painted in his spare time. George kept up the interest in stamps and he was certainly an accomplished artist. He painted many of the sea-birds he saw on his travels but his paintings became really well known at Spurn, not only for the ones he did there, some of which have been used on the covers of various publications, but also for the others he brought for sale. Many Spurn regulars must have examples of his work.

George had always had time to encourage an interest in birds and wildlife, especially in younger people. Frank Murgatroyd of Sowerby Bridge will always be grateful for his encouragement during the early days of the Halifax Zoological Group, taking him out locally and further afield; Frank was on the 1936 trip to Spurn. Dennis Furnell who worked at the R.S.P.B. in the 1950s remembers his time with George seemingly as if it was yesterday. 'He was a small man with a big personality and a big voice. He was a great influence and encouragement. He was a one-off, in the forefront of cinephotographers, the first of the really fine wildlife cameramen.' Between 1952 and 1956, he organised a week at Spurn each year for members of the Junior Bird Recorders' Club (now the Young Ornithologists' Club).

The following appreciation by Roy Crossley, who grew up in Halifax, must express some of the feelings of all who knew George:

> 'With his slightly lop-sided grin, his distinctive voice and somewhat unconventional life-style George Edwards, or 'G.R.E.' as we often called him, was a charismatic figure who had a considerable influence on those of my generation in the formative years of our youthful bird-watching.
>
> Days spent birding with George were always enlivened with an endless fund of anecdotes, usually amusing and often about the great and good of contemporary British ornithology, for George seemed to know everyone who mattered in those days. He inspired us Halifax youngsters with tales of birds beyond the hills and valleys of our industrial West Riding, and those of us in the Halifax Junior Bird Watchers' Group in the 1940s who fell under the spell of his leadership have cause to be grateful for his guidance and teaching, for he was a first rate ornithologist and tutor.
>
> Later on, when National Service took me to the Cotswolds, George provided introductions to the local big-wigs who helped me to get the best out of my birding there and later, when I went to Egypt, he was the person to whom I sent descriptions of unidentified birds, being without adequate books in those pre-field-guide days, and there was usually a prompt and always helpful reply, together with news from the home birding front.
>
> When I returned in 1953, George had gone to London to work for the R.S.P.B. and we rarely met after that. But some years ago I heard that he was in brief residence at Spurn and I went down the next free day that I had and managed to find him at Warren Cottage. We had a chat about old times and, apart from looking a bit older, he hadn't changed a bit – the old sparkle I knew and loved as a teenager was still there; he still had comic tales to tell!'

We mourn the passing of a fine ornithologist and amiable companion who will long be remembered and extend our sympathies to his sister and family.

John Cudworth

BOOK REVIEWS

Desert Sea: Fauna of the Saudi-Arabian Red Sea Coast by **Hagen Schmid**. Pp. 203, full colour photographs throughout. Hagen Schmid & Gazelle Book Services, Lancaster. 2nd edition, 1997. £28.99.

This is an unashamedly glossy book designed, primarily, to make one gasp at the sheer beauty of the Saudi Arabian Red Sea. There is virtually no text, but the photographs are truly excellent. The book also has an interesting and attractive arrangement whereby the photographs (one per page) do not fill the entire page, but are placed on a background of faint black and white images showing desert sands, corals or palm leaves.

It is a shame, perhaps, that the rationale in producing the book appears to have been to accommodate the best available photographs and not to provide a more systematic coverage of this fascinating region. There are, for example, nearly 130 images of reef fish, but only about 35 photographs of other reef organisms or scenes. This despite the fact that the Red Sea has a fantastic (and photogenic) diversity of marine invertebrates (see, for example, Peter Vine's excellent *Red Sea Invertebrates*). The final section of photographs moves onto the land, with some fascinating photographs of wildlife, people and scenery from the coastal zone.

Although good field guides do exist describing the marine and terrestrial fauna of the Red Sea, it is still rather disappointing that the text is so minimal. Short paragraphs, scattered somewhat haphazardly throughout the book, do tell some of the interesting stories about particular creatures or scenes, but the lack of structure to the book leaves one feeling that much is missing. Overall however, this is a book about pictures, and as such is a great success: they are all works of art, and fantastically reproduced.

MDS

Coral Reef Fishes: Caribbean, Indian Ocean, and Pacific Ocean including the Red Sea by **Ewald Lieske** and **Robert Myers**. Pp. 400, including 175 colour plates. Princeton University Press, 1996. Hardback $35.00.

This book, originally published in 1994 as the *Collins Pocket Guide to Coral Reef Fish*, presents an excellent field-guide to coral reef fishes anywhere in the world.

A short introductory text provides a useful background summary, describing the reef environment and various aspects of reef fish biology, ecology, biogeography and behaviour. There are over 4,000 coral reef fish worldwide, but a large number of these are very small or cryptic and are therefore unlikely to be seen, or at least noticed, by most observers. This work deliberately ignores such species and provides a remarkably comprehensive coverage of the remainder. Over 2,000 species are described and illustrated, with depictions of different forms – male, female and immature, or geographical varieties – for some species. Text descriptions are necessarily brief (10-15 species described per page), but useful and accurate. The illustrations themselves are very good indeed, with colours being very true to life in almost all cases, and with remarkable attention to detail, particularly for the salient identifying features. (N.B. The text and the illustrations for plates 134 and 135 have been switched. This error is present in all three editions so far published!)

Books on reef fish in particular countries or regions are increasingly available, many being well illustrated with colour photographs. This book, however, fills a niche for amateur and professional visitors to reefs, combining in one compact volume what has previously required several, usually expensive, works. The full identification of many reef fish from underwater sightings alone is often difficult, but not impossible. Using this book as a first point of reference will be sufficient for many users, while others may wish to combine it with other works, particularly those showing reef fish *in situ* with colour photographs, to provide a more secure base for reef fish identification.

MDS

Basic Geological Mapping by **John Barnes**. Pp. x + 133, with 45 maps and diagrams and 23 b/w photographs. 3rd edition. John Wiley. 1995. £11.99.

This sturdy, conveniently sized paperback provides a wealth of good advice on how to measure, record, and write reports of geological field observations. It is clearly targeted at students with a grasp of basic geological concepts but little experience in field recording and who need to collect their own field data.

It provides sound information on suitable equipment and commonly available types of geological maps and briefly outlines the principles of cadestral surveying. There are excellent chapters covering field measurements and techniques of rock description and on maintaining an effective fieldbook. Advice is given on preparing reports and geological sections and the whole is rounded off with guidance on field safety.

The recent trend in geological, geographical and environmental sciences towards reduced field teaching suggests that there should be a substantial number of students who would benefit from this book, as its simple, clear common sense approach is appropriate not only to geologists, but to a wide range of people who would profit from advice on how to collect field data.

DEC

The Birdwatcher's Guide to Hawai'i by **Rick Soehren**. Pp. 215, with many b/w and 19 colour photographs and 7 maps. University of Hawai'i Press. 1996. $17.95.

Another book in the now very popular series of birdwatching guides. The Hawai'ian archipelago is made up of 132 islands and this guide deals with six of the eight main ones (two being private and out of bounds) which make up over 99% of the total land area. Each island is dealt with in detail, including a check list of birds for each and listing the best birdwatching locations (O'ahu 13, Kaua'i 6, Big Island (Hawai'i) 8, Maui 6, Malaka'i 4 and Lana'i 3). Each site chapter is very comprehensive, including access details and the species most likely to be seen at any particular season. There are short chapters on the habitats, conservation, accommodation, transport and organised hikes. Written by an American who knows the area very well, the book is inevitably aimed at the American market and it is a pity that few British birdwatchers will venture to this remote part of the world, particularly so now that this guide is available, but, for those lucky enough to get there, for whatever reason, this guide is essential.

JRM

The Birds of the Northallerton and Richmond Area by **N. J. Morgan**. Pp. 76, with line drawings. Privately published, Ainderby Steeple, 1996. £3.00 paperback.

This booklet arose from the author's keen interest in the area and his desire to produce a base-line document for future researchers and he is to be commended for his effort.

The introduction is followed by brief details of the 13 major birdwatching sites in the region (with map references) and a short review of the area's birdwatchers, past and present. The classified list takes up 67 of the 76 pages and deals with 260 species, 130 of which have bred. Each species is thoroughly documented with status, favoured sites and historical details, and local names are given for some.

A most worthwhile project and having regard for the amount of research required for even a small booklet like this, well worth the bargain price of £3.00.

JRM

Microfungi on Land Plants: an Identification Handbook by **Martin B. Ellis** and **J. Pamela Ellis**. Pp. x + 868, incl. 213 pages of line drawings. Richmond Publishing, Slough. 1997. £60 hardback, £40.00 paperback.

A much revised and enlarged edition of a standard work published in 1985 by Croom Helm which, due to its success, went out of print in 1992. Its return will be welcomed by mycologists and plant pathologists for it is unparalleled in terms of its identification value in both the field and laboratory. Although concentrating on the British Isles, it will prove useful in many north temperate countries, especially in Europe and North America. Through keys, descriptions and exquisite line drawings, this work deals with *c.* 3500 species, including rusts, smuts, powdery mildews, discomycetes, pyrenomycetes, loculoascomycetes, hypomycetes and coelomycetes in sufficient detail for accurate determination. A glossary and indexes to fungi and host plants are also provided. This indispensable landmark in mycological literature is both a practical guide and a reference source and is therefore strongly recommended to both field workers and libraries.

MRDS

CONTRIBUTORS

Abbott, P. P. 64-65
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